



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

## Monograph

[urn:lsid:zoobank.org:pub:5571E5E4-47CC-43FB-B5AC-7388E403A73E](https://zoobank.org/pub:5571E5E4-47CC-43FB-B5AC-7388E403A73E)

# The deep-sea species of Triphoridae (Gastropoda, Triphoroidea) from Guadeloupe, sampled by the Karubenthos 2 expedition

Maurício Romulo FERNANDES

Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Av. Pasteur, 458, Urca, 22290-240, Rio de Janeiro, Brazil.

Email: [mauriciofernandes14@hotmail.com](mailto:mauriciofernandes14@hotmail.com)

[urn:lsid:zoobank.org:author:3B8B864F-3300-45B2-8D1F-61F282F83CDE](https://zoobank.org/author:3B8B864F-3300-45B2-8D1F-61F282F83CDE)

**Abstract.** This study aims to evaluate the taxonomic composition of the deep-sea triphorids from Guadeloupe obtained by the Karubenthos 2 expedition, which comprised 159 marine sampling events. The Karubenthos 2 sampled 14 deep-sea species of Triphoridae (i.e., species typically found below 200 m), which increases the number of deep-sea triphorids from Guadeloupe to 15. Three new species are described (*Strobiliger* *picta* sp. nov., *S. variabilis* sp. nov., *S. cupella* sp. nov.), six species were previously known only from the northern Caribbean or adjacent areas, one species (*S. cf. delicata* Fernandes & Pimenta, 2014) was previously known from SE Brazil, another species (*S. dinea* (Dall, 1927)) is widespread in the West Atlantic and only “*Inella*” *longissima* (Dall, 1881) was already recorded from Guadeloupe; two other morphs (*Strobiliger* sp. A, *Strobiliger* sp. B) remain without specific determination, requiring additional material. I formalize *Norephora* Gründel, 1975 syn. nov. as a junior synonym of *Subulophora* Laseron, 1958, which is probably related to *Inella* Bayle, 1879, but *Strobiliger* Dall, 1924 is regarded as a recent and derived group, restricted to deep waters of the Atlantic Ocean. Other taxonomic novelties in this study are: *Costatophora numerosa* (Jousseume, 1898) comb. nov.; *Euthymella sculpta* (Hinds, 1843) comb. nov.; *Strobiliger* *carioca* sp. nov. (described from SE Brazil); *Strobiliger* *colon* (Dall, 1881) comb. nov.

**Keywords.** Biodiversity, *Inella*, Lesser Antilles, *Strobiliger*, taxonomy.

Fernandes M.R. 2024. The deep-sea species of Triphoridae (Gastropoda, Triphoroidea) from Guadeloupe, sampled by the Karubenthos 2 expedition. *European Journal of Taxonomy* 972: 1–52.

<https://doi.org/10.5852/ejt.2024.972.2763>

## Introduction

Triphoridae Gray, 1847 is a family of marine microgastropods that are mostly sponge-feeders, with hundreds of described species and many yet unnamed (Bouchet *et al.* 2002; Albano *et al.* 2011; Bakker & Albano 2022). The taxonomy of triphorid species from the West Atlantic has been intensively studied in the last decades, both for the Caribbean (e.g., Rolán & Fernández-Garcés 2007, 2008, 2015; Redfern 2013; Fernandes 2024) and Brazil (e.g., Fernandes & Pimenta 2019a, 2019b, 2020; Fernandes *et al.* 2021). However, most efforts were on shallow-water species, with few studies including species from the continental slope (e.g., Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2019a, 2020), regarding

Triphoridae as absent from abyssal depths (Fernandes & Pimenta 2017). Most deep-sea triphorids from the West Atlantic were described by Dall (1881, 1889a, 1927), mainly from Cuba and Southeast USA, and based on empty shells only (sometimes worn). They are mainly assigned to *Inella* Bayle, 1879 and *Strobiligera* Dall, 1924, despite uncertainties surrounding both genera (such as the artificial group “pseudo *Inella*” – Fernandes & Pimenta 2019a). In addition, some deep-sea species from the West Atlantic with unknown protoconch are placed in the catch-all taxon *Triphora* Blainville, 1828, and one species in *Monophorus* Grillo, 1877 (Fernandes & Pimenta 2020).

Rolán & Fernández-Garcés (2015) studied the shallow-water triphorids from Guadeloupe sampled by the Karubenthos 1 expedition in 2012. Most of their identifications were followed by Lamy & Pointier (2018), who also illustrated six deep-sea species (i.e., sampled mostly below 200 m) from Guadeloupe, namely *Inella* aff. *harryleei* Rolán & Fernández-Garcés, 2008, *I. longissima* (Dall, 1881), *Triphora* sp. 1, *Triphora* sp. 2, *Triphora* sp. 3 and *Triphora* sp. 4. Lamy & Pointier (2018) also illustrated one deep-sea species from Martinique, namely *Inella triserialis* (Dall, 1881). Fernandes (2024) studied the shallow-water triphorids from Martinique, sampled by the Madibenthos expedition, but also included shallow-water species (i.e., mostly found above 200 m) from Guadeloupe, sampled by the Karubenthos 1 and Karubenthos 2 expeditions; nine typical shallow-water species were obtained by Karubenthos 2.

The Karubenthos 2 expedition was conducted around Guadeloupe in June 2015 and organized jointly by the MNHN (Muséum national d’Histoire naturelle, France), the Université des Antilles et de la Guyane and the Guadeloupe National Park. Its aim was to generate a robust inventory of the local deep-sea benthos (Poupin & Corbari 2016). On board the R/V *Antea*, 159 sampling events were performed around the archipelago, of which 130 used a Warén dredge (proper for hard substrata) and 29 a benthic beam trawl (soft substrata), comprising 13 stations with depths between 50 and 100 m and 146 stations between 100 and 900 m (Poupin & Corbari 2016). Previous studies revealed new deep-sea species of gastropods based on the material sampled by Karubenthos 2 (e.g., Garrigues & Lamy 2017; Rabiller & Richard 2019; Harasewych *et al.* 2020).

The objective of this study is to evaluate the taxonomic composition of the deep-sea triphorids from Guadeloupe obtained by the Karubenthos 2 expedition, providing a basis for future studies on this taxonomically challenging group.

## Material and methods

Stations in which triphorids were obtained during the Karubenthos 2 expedition are listed under each species; station data can be found in [collections.mnhn.fr/RPSL](https://collections.mnhn.fr/RPSL) and in Table 1. Worn triphorid shells that could not be identified are not listed. Shells were photographed under a Leica DFC450 camera coupled to a Leica M205C stereo microscope (Museu Nacional, Universidade Federal do Rio de Janeiro/MNRJ) or to a Nikon D5000 camera coupled to a Leica MZ16 stereo microscope (MNHN). Owing to the broad morphological variation and depth range of some species, I profusely illustrated them in order to represent the observed variation as well as possible.

The type material of most deep-sea triphorids from the Caribbean was recently illustrated by Rolán & Fernández-Garcés (2008) and Fernandes & Pimenta (2019a), enabling comparisons with the species sampled from the Karubenthos 2 expedition. Descriptions are solely based on the examined material, following procedures described by Fernandes & Pimenta (2015a, 2019a, 2019b); the apical angle of early whorls was measured following Gofas *et al.* (2023). Empty shells and live specimens are respectively indicated in the material examined by ‘sh’ and ‘spec./specs?’, some live specimens are indicated as ‘stored dry’ when dried soft parts are observed through the teleoconch. The few specimens with soft parts and properly preserved in ethanol had their foot removed for DNA procedures (unpublished data);

**Table 1.** Localities, coordinates, depths and dates of stations in which deep-water triphorids were sampled from Guadeloupe by the Karubenthos 2 expedition.

Station	Locality	Latitude	Longitude	Shallowest depth (m)	Maximum depth (m)	Date
DW4508	W Basse-Terre	16°13' N	61°54' W	523	674	7 Jun. 2015
CP4513	W Basse-Terre	16°13' N	61°54' W	406	644	8 Jun. 2015
DW4536	N Grande-Terre	16°40' N	61°28' W	323	347	12 Jun. 2015
DW4538	N Grande-Terre	16°38' N	61°31' W	320	338	12 Jun. 2015
DW4544	N Grande-Terre	16°38' N	61°37' W	413	423	13 Jun. 2015
DW4549	N Grande-Terre	16°38' N	61°35' W	343	402	14 Jun. 2015
DW4550	N Grande-Terre	16°37' N	61°31' W	432	482	14 Jun. 2015
DW4554	E La Désirade	16°21' N	60°56' W	300	370	15 Jun. 2015
DW4555	E La Désirade	16°24' N	60°51' W	100	258	15 Jun. 2015
DW4556	E La Désirade	16°24' N	60°49' W	367	428	15 Jun. 2015
DW4572	E La Désirade	16°19' N	60°55' W	396	399	17 Jun. 2015
DW4577	E La Désirade	16°20' N	60°54' W	358	402	18 Jun. 2015
DW4589	W Marie-Galante	15°59' N	61°27' W	150	221	21 Jun. 2015
DW4592	W Marie-Galante	15°58' N	61°22' W	201	214	22 Jun. 2015
DW4599	W Marie-Galante	15°53' N	61°25' W	262	266	22 Jun. 2015
DW4600	N Marie-Galante	16°02' N	61°18' W	557	680	23 Jun. 2015
DW4601	N Marie-Galante	16°02' N	61°17' W	346	632	23 Jun. 2015
DW4613	E La Désirade	16°25' N	60°50' W	210	240	25 Jun. 2015
DW4615	E La Désirade	16°23' N	60°50' W	226	270	25 Jun. 2015
CP4618	E La Désirade	16°21' N	60°45' W	780	828	25 Jun. 2015
DW4634	W Marie-Galante	15°48' N	61°26' W	304	310	27 Jun. 2015
DW4635	W Marie-Galante	15°50' N	61°26' W	265	268	27 Jun. 2015
DW4637	S Marie-Galante	15°52' N	61°20' W	217	225	28 Jun. 2015
DW4638	S Marie-Galante	15°50' N	61°19' W	305	312	28 Jun. 2015
DW4646	S Marie-Galante	15°51' N	61°18' W	250	254	29 Jun. 2015
CP4649	W Marie-Galante	16°02' N	61°27' W	367	389	29 Jun. 2015

operculum, jaw and radula were extracted when possible, and imaged through a JEOL 6490-LV SEM (scanning electron microscope). In figure captions, shell size refers to length.

Because most dredging events involved wide depth ranges, the bathymetric distributions of the triphorids sampled by Karubenthos 2 are probably unrealistic. For example, a species sampled in a dredging station between 200 and 400 m does not necessarily live within this entire depth range. Nevertheless, the entire depths are provided. I disregarded depth ranges from stations in which all shells were heavily worn (i.e., probably derived from post-mortem dislodgement).

In order to properly compare material from Karubenthos 2 with records from the literature, one species previously recorded from Brazil by Fernandes & Pimenta (2019a) as *Inella apexbilirata* Rolán & Fernández-Garcés, 2008 is here described as new, at the end of the Results section.

The abundance distributions of triphorids from Karubenthos 2 were obtained using the software PAST ver. 4.02, regarding the total number of shells/specimens sampled at depths below 100 m. The coverage-based rarefaction and extrapolation of triphorids from Karubenthos 2, as well as the sample coverage (index SC), were calculated with the online version of the iNEXT package (<https://chao.shinyapps.io/iNEXTOnline/>), using 100 bootstrap replications and a confidence interval equal to 0.95; for both, I did not consider the few shells from the five shallow-water species sampled by Karubenthos 2 (at stations below 100 m) and indicated in Fernandes (2024), namely *Cosmotriphora melanura* (C.B. Adams, 1850), *Iniforis turrithomae* (Holten, 1802), *Metaxia rugulosa* (C.B. Adams, 1850), *Sagenotriphora osclausum* (Rolán & Fernández-Garcés, 1995) and *Similiphora intermedia* (C.B. Adams, 1850), whereas I did consider the abundance distribution. The number of triphorid species sampled per station included the above mentioned shallow-water species, whereas the number of Karubenthos 2 stations in which each triphorid species was sampled did not (i.e., only the species illustrated in this study); in both cases, only depths below 100 m were considered.

List of acronyms:

FLMNH	=	Florida Museum of Natural History, Gainesville, FL, USA
IBUFRJ	=	Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
MCZ	=	Museum of Comparative Zoology, Cambridge, MA, USA
MNHN	=	Muséum national d’Histoire naturelle, Paris, France
MNRJ	=	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
NMNH/USNM	=	National Museum of Natural History, Washington D.C., USA

## Results

Class Gastropoda Cuvier, 1795  
Subclass Caenogastropoda Cox, 1960  
Superfamily Triphoroidea Gray, 1847  
Family Triphoridae Gray, 1847  
Group “**pseudo *Inella***” (see Fernandes & Pimenta 2019a)

“***Inella***” *harryleei* Rolán & Fernández-Garcés, 2008

Fig. 1

*Inella harryleei* Rolán & Fernández-Garcés, 2008: 105, fig. 13a–k.

“*Inella*” *harryleei* – Fernandes & Pimenta 2019a: fig. 3k–l; 2019b: 46, figs 2l, 30–32.

*Inella harryleei* – Leal 2021: 6, fig. 38.

## Type material

### Holotype

USA • sh; Florida, off Dry Tortugas; depth 90 m; FLMNH 419182.

### Paratypes

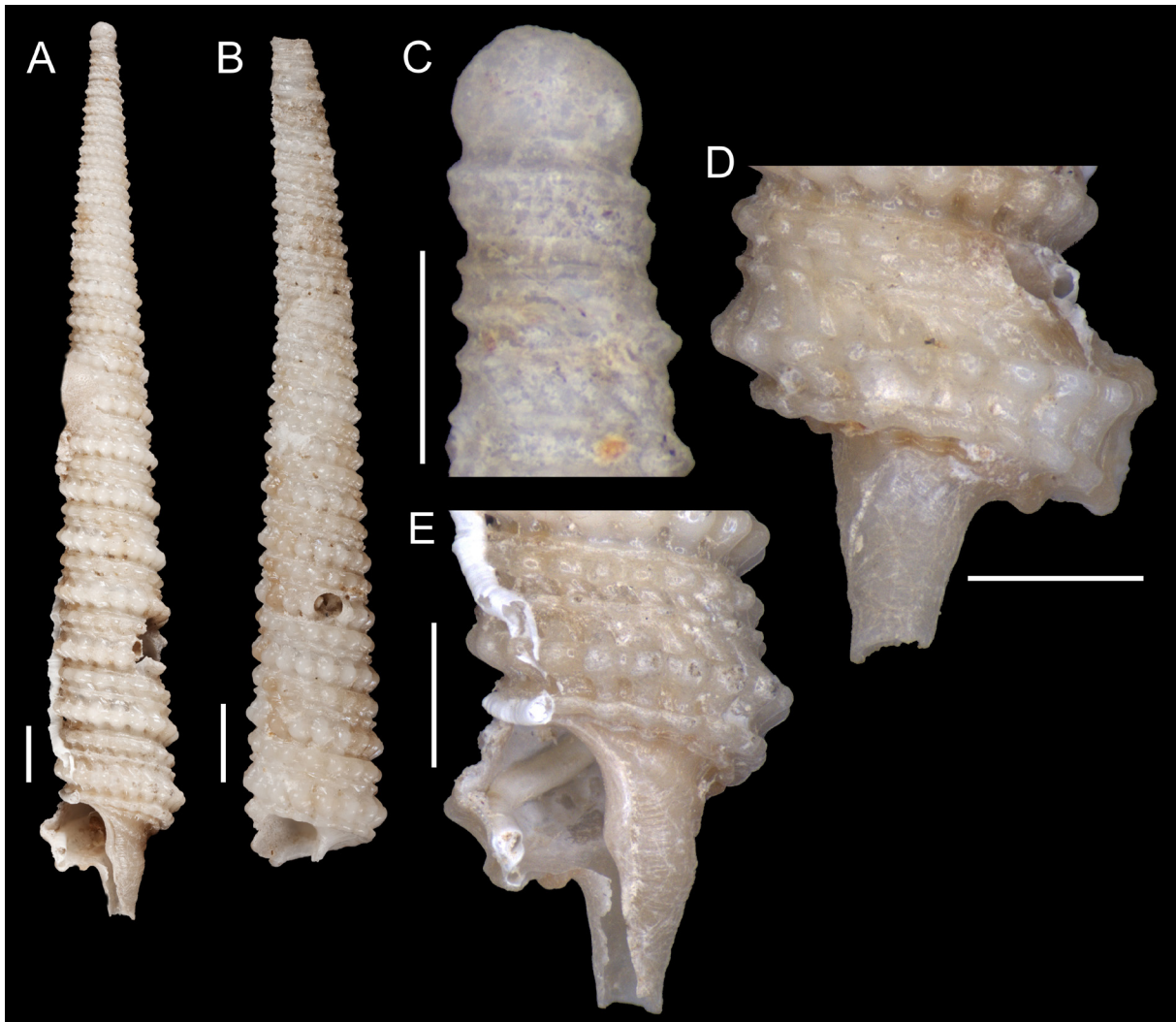
See Rolán & Fernández-Garcés (2008).

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 2 sh; stn DW4592; MNHN.

**Emended description**

Shell sinistral, conical-fusiform, up to 15.9 mm long, 2.4 mm wide, length/width ratio 6.6, apical angle of early whorls 11°. Protoconch paucispiral, three whorls, 0.96 mm long, 0.57 mm wide; first whorl smooth, inflated, only slightly narrower than subsequent whorls, which have two thin, nearly smooth spiral cords, situated at 33% and 76% of last whorl height; transition to teleoconch nearly indistinct. Teleoconch with up to 20 whorls; two spiral cords (adapical and abapical) in beginning of teleoconch, continuous to those of protoconch, but abapical one considerably more developed until body whorl; median spiral cord emerges very narrowly at end of second whorl, slowly developing but never reaching same size as other cords; suture shallow, with a smooth to slightly wavy sutural cord; 16–17 opisthocline axial ribs on 12<sup>th</sup> teleoconch whorl; medium to large-sized (on abapical cord), rounded to slightly elliptical nodules; nodulous, moderately thin subperipheral cord, with a slightly nodulous adapical basal cord right below it and a thin, nearly smooth abapical basal cord situated apart; no evident



**Fig. 1.** *“Inella” harryleei* Rolán & Fernández-Garcés, 2008. A–E. MNHN, stn DW4592, 15.9 mm, 10.6 mm. Scale bars: A–B, D–E = 1 mm; C = 500 µm.

supranumerical cord; nearly rounded aperture, 1.1 mm long, 0.84 mm wide, length/width ratio 1.3; anterior canal very long, partially open, directed downward, 1.0 mm long, 0.45 mm wide, length/width ratio 2.3. Shell mainly white, stained by few and discrete light brown (or cream) axial patches, usually comprising width of one or two axial ribs.

### Remarks

The only known protoconch of “*I.*” *harryleei* from Guadeloupe (Fig. 1C) has a first whorl apparently more inflated than those illustrated in the original description, from Florida and Louisiana (USA), although all other shell features are very similar. Based on the nearest record from the Florida Keys (Rolán & Fernández-Garcés 2008), the present record extends the known range of “*I.*” *harryleei* by ~2180 km into the Caribbean. However, Rolán & Fernández-Garcés (2008) indicated a shell fragment from the ‘West Indies’ as possibly belonging to this species.

Lamy & Pointier (2018: 284, pl. 91 fig. 7a–b) identified a shell from Guadeloupe as *Inella* aff. *harryleei*, following the morph from Florida illustrated by Rolán & Fernández-Garcés (2008) under this name. In fact, the teleoconch of this shell from Guadeloupe differs from that of “*I.*” *harryleei* (see Rolán & Fernández-Garcés 2008 for further details). Moreover, this shell has an abapical spiral cord that is even more prominent than that of “*I.*” aff. *harryleei* from Florida. Unfortunately, the broken apex of the shell from Guadeloupe precluded further comparisons. Lamy & Pointier (2018) indicated a depth range of 55–360 m for this morph; considering that “*I.*” aff. *harryleei* from Florida is only known from 55 m (Rolán & Fernández-Garcés 2008), only the depth of 360 m is confidently assigned to this peculiar shell from Guadeloupe.

### Geographic distribution

USA: Florida (Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2019b), Louisiana (Rolán & Fernández-Garcés 2008; Garcia & Lee 2020); Guadeloupe (this study).

### Bathymetric distribution

Empty shells previously known from 46–500 m (Rolán & Fernández-Garcés 2008), live specimens only known from 63 m (Fernandes & Pimenta 2019b). This study: 201–214 m (empty shells).

### “*Inella*” *longissima* (Dall, 1881) Figs 2–5

*Triforis* (*Ino*) *longissimus* Dall, 1881: 80.

*Triforis* (*Inella*) *longissima* – Dall 1889a: 246, pl. 20 fig. 10; 1889b: 138, pl. 20 fig. 10.

*Triphora longissima* – Abbott 1974: 112, fig. 1138 (a reproduction of Dall’s illustration).

*Inella longissima* – Garcia & Lee 2002: 11. — Rolán & Fernández-Garcés 2008: 100, figs 10, 36d (the latter is a reproduction of Dall’s illustration). — Rosenberg *et al.* 2009: 645. — Lamy & Pointier 2018: 286, pl. 91 fig. 8a–b.

“*Inella*” *longissima* – Fernandes & Pimenta 2019a: fig. 3j.

non *Inella triserialis* Dall, 1881 – Lamy & Pointier 2018: 286, pl. 91 fig. 9.

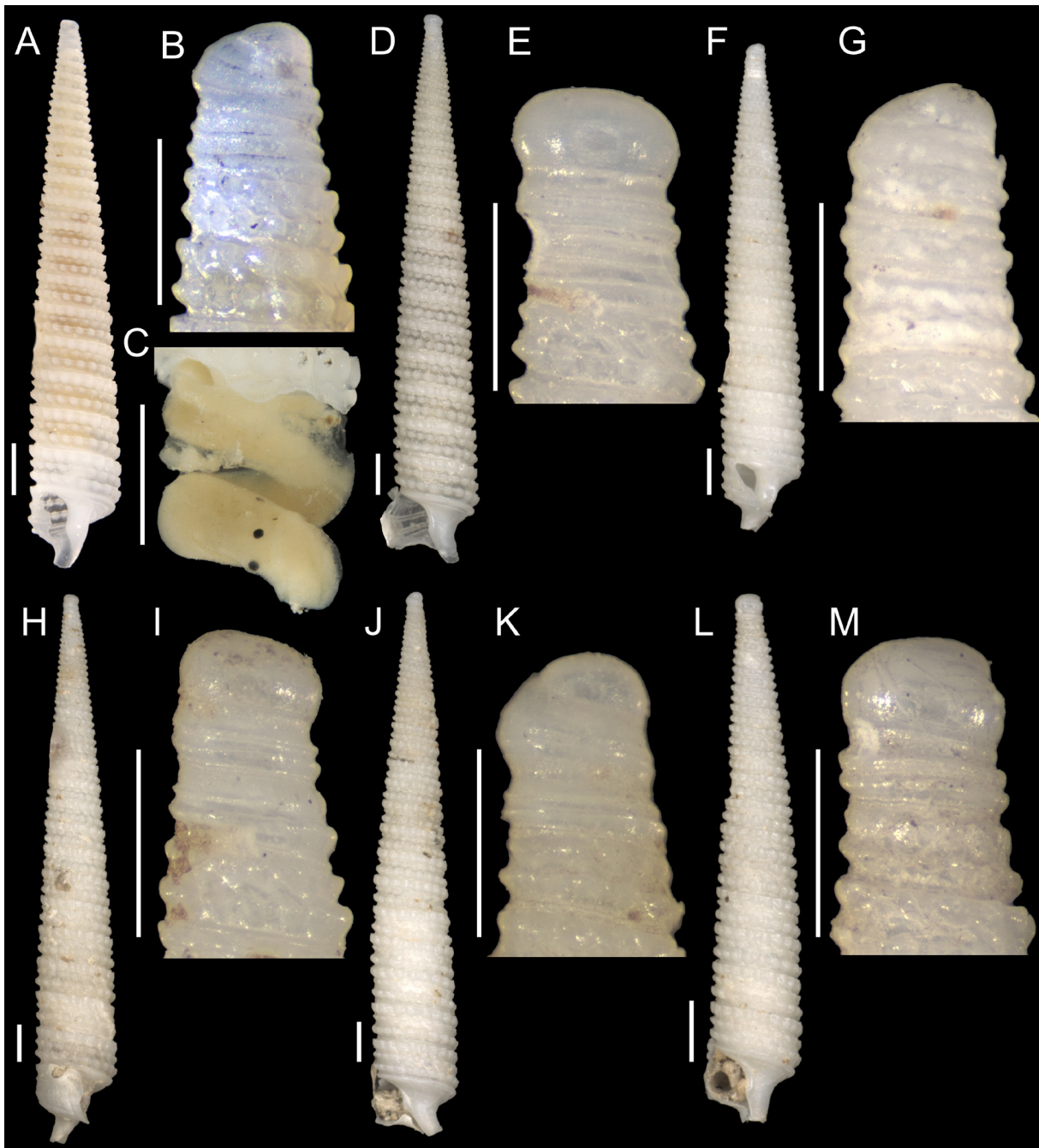
### Type material

#### Lectotype

CUBA • sh; off Havana; 23°09′00″ N, 82°21′30″ W; depth 320 m; Blake 1877–1878 Exped.; MCZ 7381.

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 2 sh, worn; stn DW4508; MNHN • 16 sh and 1 spec. stored dry; stn DW4549; MNHN • 2 sh; stn DW4550; MNHN • 5 sh; stn DW4554; MNHN • 9 sh and 1 spec. stored in ethanol; stn DW4555; MNHN-IM-2019-20012 (for the live specimen) • 1 sh; stn DW4556; MNHN • 2 sh; stn DW4572; MNHN • 3 sh; stn DW4577; MNHN • 1 sh; stn DW4589; MNHN • 5 sh; stn DW4592; MNHN • 18 sh and 2 spec. stored dry; stn DW4613; MNHN • 1 sh and

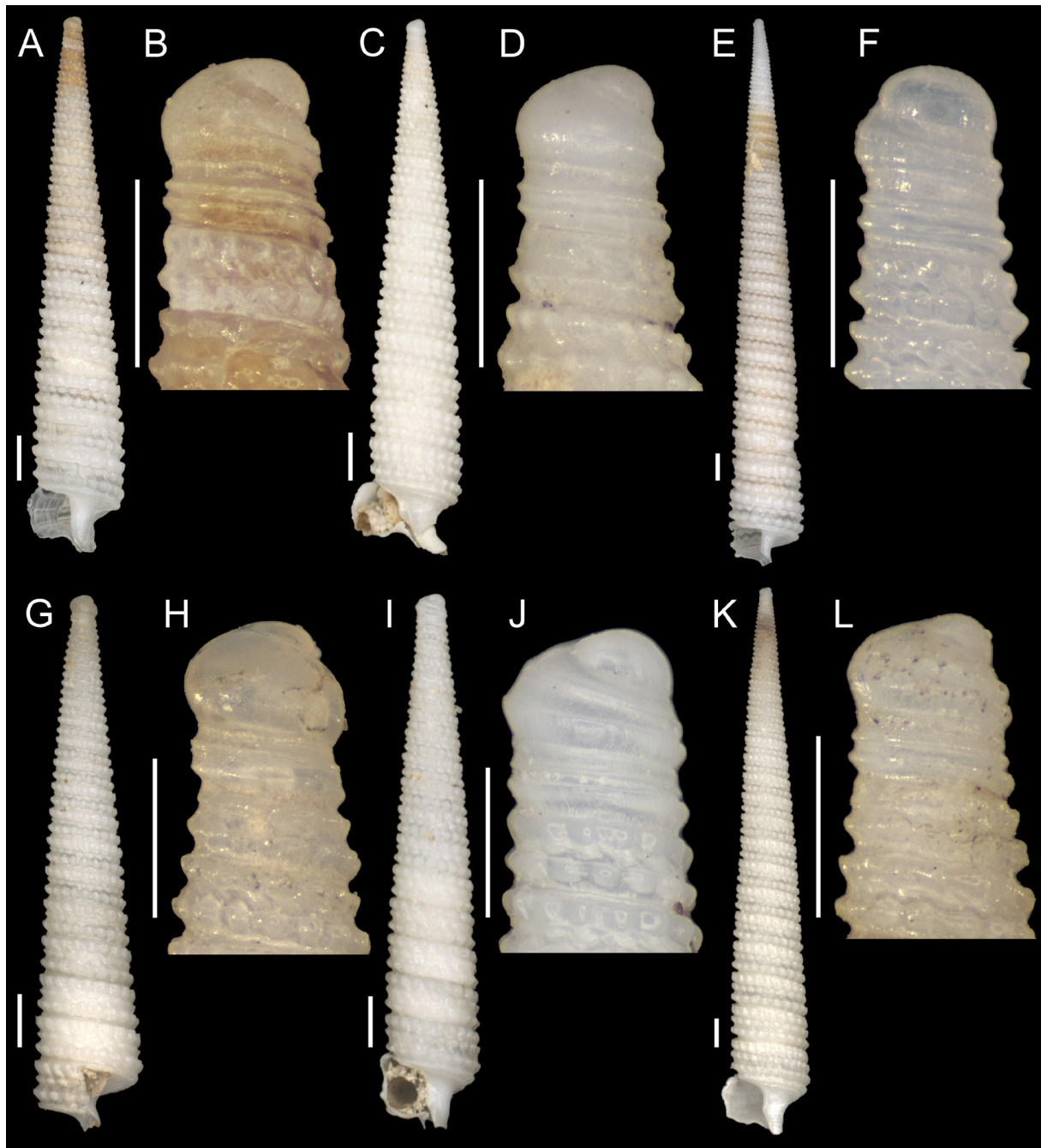


**Fig. 2.** *“Inella” longissima* (Dall, 1881). **A–C.** MNHN-IM-2019-20012, stn DW4555, 10.6 mm. **D–G.** MNHN, stn DW4555, 13.4 mm, 10.5 mm. **H–M.** MNHN, stn DW4549, 14.7 mm, 13.6 mm, 8.7 mm. Scale bars: A, C–D, F, H, J, L = 1 mm; B, E, G, I, K, M = 500  $\mu$ m.

1 spec. stored dry; stn DW4615; MNHN • 5 sh; stn DW4634; MNHN • 1 sh; stn DW4637; MNHN • 8 sh; stn DW4646; MNHN.

### Emended description

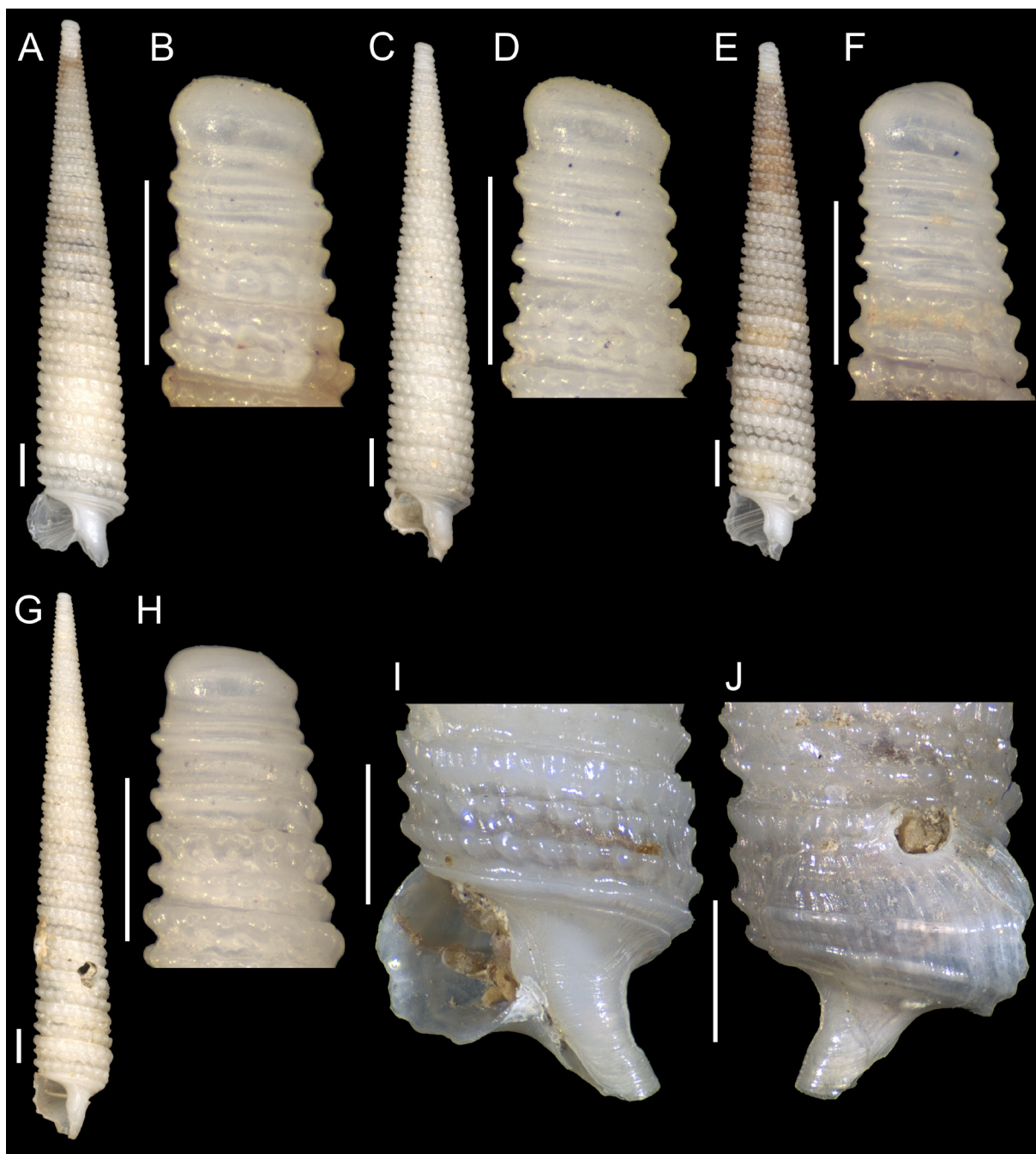
Shell sinistral, conical-fusiform, up to 20.1 mm long (adult shells reach at least 8.7 mm in length), 2.8 mm wide, length/width ratio 5.5–7.1, apical angle of early whorls 13–15°. Protoconch paucispiral,



**Fig. 3.** “*Inella*” *longissima* (Dall, 1881). **A–D.** MNHN, stn DW4549, 11.9 mm, 11.2 mm. **E–F.** MNHN, stn DW4613, 20.1 mm. **G–J.** MNHN, stn DW4550, 10.0 mm, 10.5 mm. **K–L.** MNHN, stn DW4572, 19.0 mm. Scale bars: A, C, E, G, I, K = 1 mm; B, D, F, H, J, L = 500 μm.

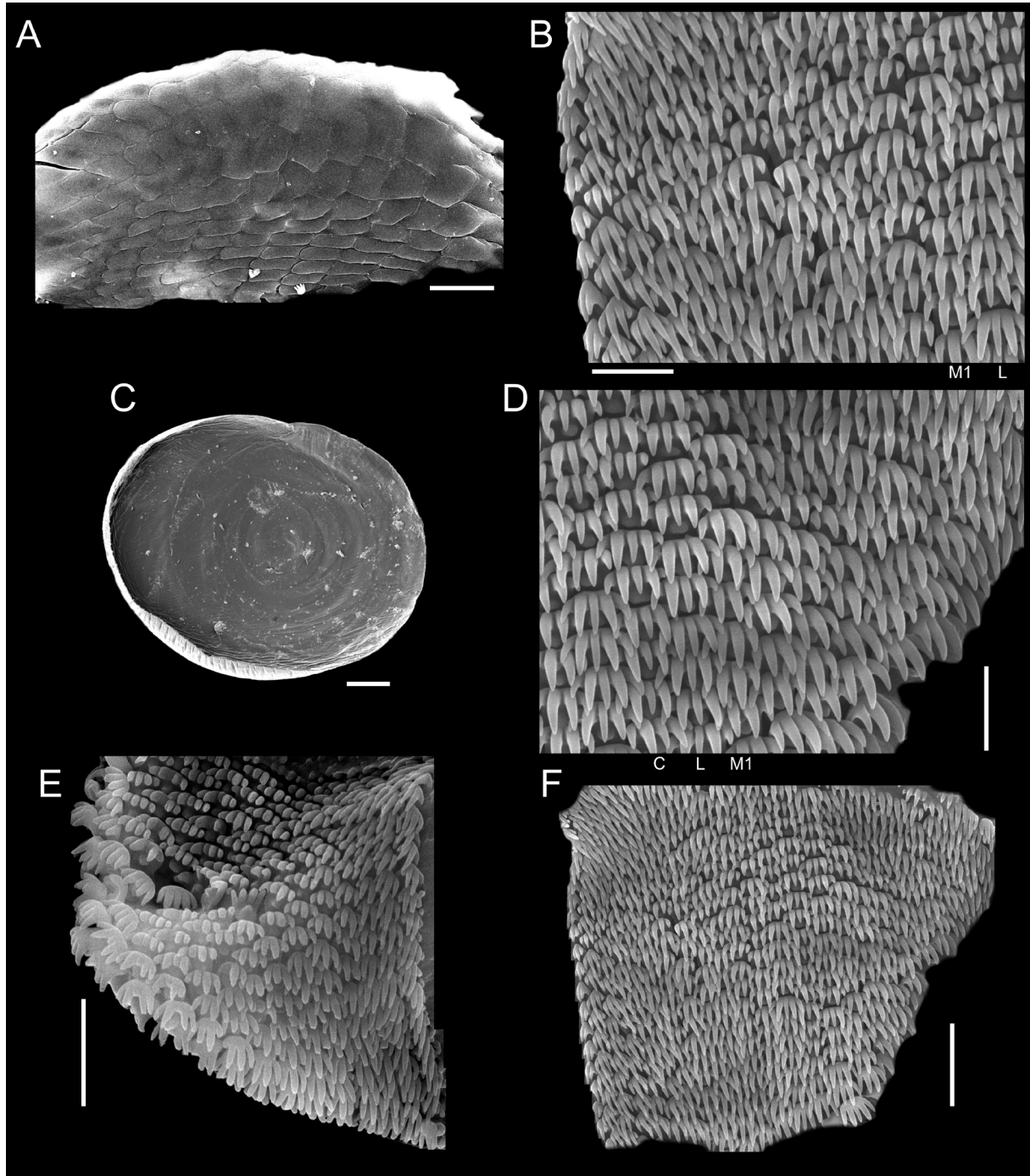


2.5–3.0 whorls, 0.55–0.64 mm long, 0.42–0.62 mm wide; first whorl smooth, slightly to considerably inflated, sometimes with same width as subsequent whorls; subsequent whorls with two main spiral cords (situated at 35–44% and 65–70% of last whorl height), the abapical one slightly to considerably more prominent, in addition to a narrow subsutural cord; transition to teleoconch gradual, nearly indistinct. Teleoconch with up to 30 whorls; two spiral cords (adapical and abapical) in beginning of teleoconch, continuous with those of protoconch; median spiral cord emerges narrowly between fourth and eighth



**Fig. 4.** “*Inella*” *longissima* (Dall, 1881). **A–D.** MNHN, stn DW4613, 12.8 mm, 10.8 mm. **E–F.** MNHN, stn DW4615, 11.2 mm. **G–H.** MNHN, stn DW4637, 16.0 mm. **I–J.** MNHN, stn DW4549 (same shell as Fig. 2H). Scale bars: A, C, E, G, I–J = 1 mm; B, D, F, H = 500  $\mu$ m.

whorls, bordering close to adapical cord and slowly developing, reaching nearly same size as abapical cord (adapical one more prominent) only in body whorl of large shells; suture shallow, with a small sutural cord; 19–21 opisthocline axial ribs on 12<sup>th</sup> teleoconch whorl; medium-sized, rounded to slightly elliptical nodules; nearly smooth subperipheral cord, with one or two smooth, very thin basal cords right below subperipheral cord; a weak supranumerical cord may form between median and abapical spiral



**Fig. 5.** *Inella* *longissima* (Dall, 1881), MNHN-IM-2019-20012, stn DW4555. **A.** Outer jaw. **B, D–F.** Radula. **C.** Operculum. Minor letters indicate central (C), lateral (L) and first marginal (M1) teeth. Scale bars: A = 20  $\mu$ m; B, D = 5  $\mu$ m; C = 100  $\mu$ m; E–F = 10  $\mu$ m.

cords; rounded to slightly elliptical aperture, 0.88–1.24 mm long, 0.67–1.09 mm wide, length/width ratio 1.1–1.5; anterior canal can be moderately long, partially to almost closed, 0.38–0.97 mm long, 0.30–0.43 mm wide, length/width ratio 1.0–2.1; posterior canal as a deep sinus and almost detached from aperture, or as a rounded orifice, completely detached from aperture. White shell.

Large eyes. Operculum thin, semi-transparent, nearly rounded to elliptical, multispiral, nucleus sub-central, dislocated 19% from center toward margin. Jaw with scales varying in shape, but mostly rectangular (12.5–14.4 mm long, 3.5–4.0 mm wide, ratio length/width 3.3–3.8), rectangular-bilobed (11.4–16.5 mm long, 4.4–6.1 mm wide, ratio length/width 2.1–3.7) or composed of irregular, large polygons (up to 18.1 mm long), sometimes square. Radula 12-1-1-1-12, with little differentiation in teeth morphology; central tooth comb-like, with five elongated cusps, central and marginal cusps slightly shorter and thinner than cusps 2 and 4; lateral teeth comb-like, with five elongated cusps, marginal cusps slightly shorter, marginal and central cusps slightly thinner than cusps 2 and 4; M1–M11 with four elongated cusps, gradual narrowing of teeth from M1 to M11, as well as shortening of cusps 1 (especially) and 4, which are ~74% of length of cusps 2 and 3 in M1, instead of ~42% (cusp 1) or ~64% (cusp 4) of length of cusps 2 and 3 in M11; M12 reduced, with three cusps (after complete reduction of former cusp 1 in other marginal teeth), central one more elongated than lateral cusps; central tooth up to 4.0  $\mu\text{m}$  wide, lateral teeth up to 4.3  $\mu\text{m}$  wide, M1 up to 3.5  $\mu\text{m}$  wide, M12 up to 1.3  $\mu\text{m}$  wide.

### Remarks

“*Inella*” *longissima* was previously recorded from Guadeloupe (between 200 and 500 m) by Lamy & Pointier (2018). In addition, they applied the name *Inella triserialis* (Dall, 1881) to a very similar morph from Martinique. The few apparent differences between these two morphs are the smaller shell length (10 mm in the figured shell of the morph named as *I. triserialis* vs 20.7 mm in the figured shell of “*I.*” *longissima*) and the earlier development of the median spiral cord in the supposed *I. triserialis*. Adult shells from Karubenthos 2 also show a broad range in length (8.7–20.1 mm), which results in large differences with respect to where the median spiral cord of the teleoconch emerges (between the fourth and eight whorls, respectively in small and large shells). However, there is little variation in the dimensions and number of protoconch whorls (2.5–3.0), the more or less inflated first protoconch whorl and certain teleoconch features (e.g., the number of axial ribs). I cannot split the current identification of “*I.*” *longissima* from Guadeloupe in more than one species, and I regard *I. triserialis* from Martinique (Lamy & Pointier 2018) as conspecific.

The protoconch of “*I.*” *longissima* from Guadeloupe matches that of a juvenile from the Florida Keys, USA (Rolán & Fernández-Garcés 2008: fig. 10f), which was up to now the only image of a protoconch of this species. The only inconsistency between the shells from Florida, Bahamas and Cuba described by Rolán & Fernández-Garcés (2008) and those from Guadeloupe (Lamy & Pointier 2018; this study) is related to which spiral cord is slightly more prominent on the teleoconch: in the first study it is the abapical one, whereas in Guadeloupe it is the adapical one. The shell with unspecified locality shown by Rolán & Fernández-Garcés (2008: fig. 10b, g) is certainly from another species if compared to shells from Guadeloupe, with the adapical cord even weaker than the median cord in later whorls. The well-developed, almost closed posterior canal of “*I.*” *longissima* is illustrated in shells from Guadeloupe (Fig. 4J; Lamy & Pointier 2018: fig. 8b) and in the lectotype (Dall 1889a, 1889b).

Dall (1889b) put the northern limit of “*I.*” *longissima* at Cape Hatteras, North Carolina (USA), and the southern limit in Cuba (but the species is also present in the Florida Keys and in the ‘West Indies’, a term which comprises Cuba). The record from Cape Hatteras, reproduced by Abbott (1974) and Rosenberg *et al.* (2009), seems to be a mistake, because Dall (1889b) did not list the species for the so-called ‘districts’ in the respective columns, from New Jersey to Biscayne Bay (Florida). This species seems to be mostly from the Caribbean deep sea, apparently extending northwards to Louisiana, USA (Garcia &

Lee 2002, 2020; although not illustrated). The records from Brazil provided by Rios (1985, 1994, 2009) are erroneous (Fernandes & Pimenta 2019a).

There are errors in the literature in relation to the bathymetric range of “*I.*” *longissima*. Rolán & Fernández-Garcés (2008) cited 175 m as the depth for the lectotype (repeated by Bakker & Albano 2022), but Dall (1889a) indicated the depth as 175–450 fathoms (= 320–823 m). Accordingly, the coordinates cited here for the lectotype follow the MCZ Invertebrate Zoology online database (<https://mcz.harvard.edu/invertebrate-zoology-research-collection>), but not those provided by Rolán & Fernández-Garcés (2008), with a wrong latitude. Rolán & Fernández-Garcés (2008) did not provide the depth for the lots ANSP 368279 (Bahamas) and ANSP 312592 (Florida Keys), but the online database of the respective collection (<http://clade.ansp.org/malacology/collections/>) indicates respectively 500 m and 183 m (here followed). The broad depth range (73–1040 m) provided by Rosenberg *et al.* (2009) is partly erroneous, because the depth of 1040 m was based on Rios (1985, 1994, 2009), i.e., a wrong identification for shells from Brazil; the shallowest record is based on the depth range (73–402 m) which Abbott (1974) provided for this species from West Florida, and it requires confirmation because the material was not figured.

Anatomic features of “*I.*” *longissima* are herein studied for the first time. The species has well-developed eyes (Fig. 2C), considerably larger than those of *Strobiligera* species from deeper waters (Fig. 18B), suggesting that “*I.*” *longissima* is not confined to waters with a complete absence of light. The operculum with a subcentral nucleus and the radula with many, weakly differentiated comb-like teeth (but marginal teeth considerably reduced) perfectly match with the current concept of *Monophorus* Grillo, 1877 (Fernandes & Pimenta 2019b). However, an ongoing molecular phylogeny of Triphoroidea (in prep.) has raised suspicion about the monophyly of *Monophorus*, and the generic position of “*I.*” *longissima* will be discussed further.

### Geographic distribution

USA: Florida (Dall 1889b; Abbott 1974; Rolán & Fernández-Garcés 2008), Louisiana (Garcia & Lee 2002, 2020); Bahamas (Rolán & Fernández-Garcés 2008); Cuba (Dall 1889a, 1889b); Guadeloupe (Lamy & Pointier 2018; this study); Martinique (Lamy & Pointier 2018 – as *Inella triserialis*).

### Bathymetric distribution

Empty shells previously known from 73–823 m (Dall 1889b; Abbott 1974). This study: 100–482 m (empty shells), 100–402 m (live specimens).

“*Inella*” *pseudolongissima* Rolán & Fernández-Garcés, 2008

Fig. 6

*Inella pseudolongissima* Rolán & Fernández-Garcés, 2008: 102, fig. 11.

“*Inella*” *pseudolongissima* – Fernandes & Pimenta 2019a: fig. 3n.

### Type material

#### Holotype

CUBA • sh; off Havana; 823 m (as stated in the original description) or 444–823 m (as stated on the NMNH invertebrate collection website); Blake Expedition; USNM 87316.

#### Paratypes

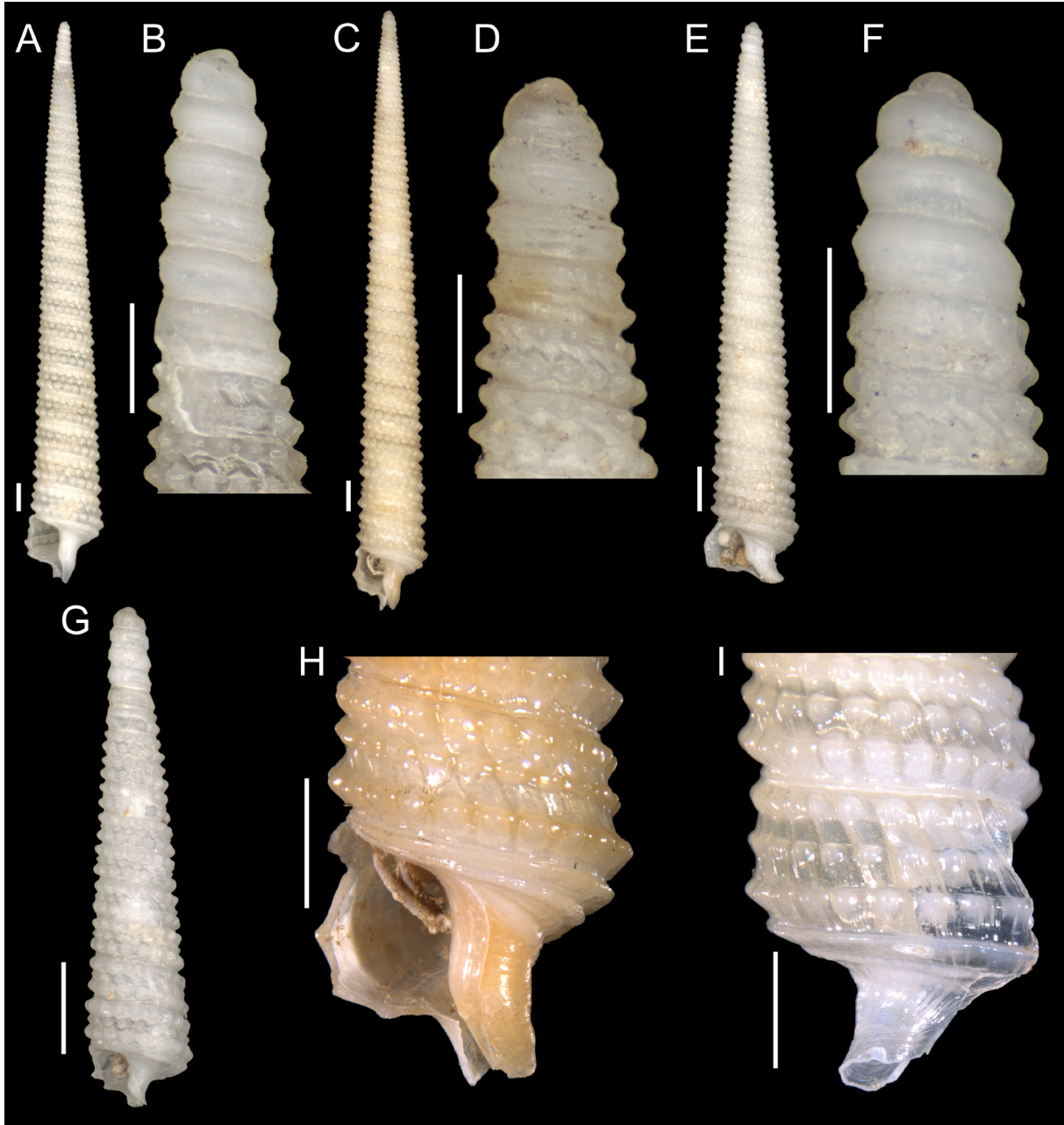
See Rolán & Fernández-Garcés (2008).

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 5 sh; stn DW4549; MNHN • 4 sh; stn DW4550; MNHN • 2 sh; stn DW4589; MNHN • 1 sh juv.; stn DW4599; MNHN • 1 sh; stn DW4601; MNHN • 1 sh; stn DW4634; MNHN.

**Emended description**

Shell sinistral, conical-fusiform, up to 19.9 mm long (adult shells reach at least 12.6 mm in length), 2.7 mm wide, length/width ratio 6.2–8.0, apical angle of early whorls 11–13°. Protoconch multispiral,



**Fig. 6.** *Inella* *pseudolongissima* Rolán & Fernández-Garcés, 2008. **A–B, I.** MNHN, stn DW4549, 19.9 mm. **C–D, H.** MNHN, stn DW4589, 19.6 mm. **E–F.** MNHN, stn DW4634, 12.6 mm. **G.** MNHN, stn DW4550, 5.4 mm. Scale bars: A, C, E, G–I = 1 mm; B, D, F = 500 µm.

columnar, 4.0–6.0 whorls, 0.84–1.48 mm long, 0.55–0.66 mm wide; first whorl smooth, not inflated; on second whorl two thin spiral cordlets appear (situated at 34–37% and 66–73% of whorl height), but abapical spiral cordlet sometimes thinner than adapical one and may appear only on third whorl; both cordlets may resemble only slight elevations in some shells instead of true cordlets due to their minute width; transition to teleoconch gradual, nearly indistinct. Teleoconch with up to 28 whorls; two spiral cords (adapical and abapical) in beginning of teleoconch, continuous with cordlets of protoconch; median spiral cord emerges narrowly between fourth and sixth whorls, bordering closely to adapical cord, slowly developing and reaching nearly same size as other cords only on body whorl (abapical cord can be slightly more developed than other cords in late whorls); suture shallow, with a smooth sutural cord; 18–19 opisthocline axial ribs on 18<sup>th</sup> teleoconch whorl; medium-sized, nearly rounded to slightly elliptical nodules; slightly nodulous to nearly smooth subperipheral cord, with a smooth, thin basal cord right below it; no supranumerical cord; elliptical aperture, 1.4–1.5 mm long, 1.0–1.3 mm wide, length/width ratio 1.2–1.3; anterior canal open to partially open, directed downward, 0.60–0.74 mm long, 0.46–0.53 mm wide, length/width ratio 1.3–1.5; posterior canal as a deep sinus, almost detached from aperture. Shell white to faintly cream.

### Remarks

The current record from Guadeloupe extends the known range of “*I.*” *pseudolongissima* by ~2300 km. Agreeing with the original description and illustrations, shells from Guadeloupe are highly variable with respect to the size and number of protoconch whorls (although always multispiral, with at least four whorls), the strength of the spiral cordlets of the protoconch and the strength of the abapical spiral cord of the teleoconch (Fig. 6). The variation in the size and number of protoconch whorls may be related to the duration of embryonal growth within the egg; see Fernandes & Pimenta (2019a) for a discussion on other triphorids with a supposed long duration of intracapsular metamorphosis, resulting in multispiral protoconchs for species with a supposed non-planktotrophic development.

### Geographic distribution

USA: Florida (Rolán & Fernández-Garcés 2008); Cuba (Rolán & Fernández-Garcés 2008); Guadeloupe (this study).

### Bathymetric distribution

Empty shells previously known from 77–823 m (Rolán & Fernández-Garcés 2008). This study: 150–632 m (empty shells).

Genus *Strobiliger* Dall, 1924

*Strobiliger* cf. *enopla* (Dall, 1927)

Figs 7–8

*Triphora (Strobiliger) enopla* Dall, 1927: 95.

*Triphora (Strobiliger) enopla* – Abbott 1974: 112.

*Inella enopla* – Rolán & Fernández-Garcés 2008: 120, fig. 18a–e.

*Strobiliger enopla* – Fernandes & Pimenta 2014: 169; 2019a: fig. 3x.

### Type material

#### Lectotype

USA • sh; ‘off Fernandina’ [but coordinates provided by Dall (1927) off Fernandina (Florida) actually match with the state of Georgia]; depth 538 m; USNM 108074. According to the NMNH invertebrate

collection website, the original label and the five paralectotypes, which should be stored in the same lot (Rolán & Fernández-Garcés 2008), are missing.

### Material examined

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4544; MNHN • 8 sh; stn DW4549; MNHN • 3 sh; stn DW4550; MNHN • 1 spec. stored dry; stn DW4555; MNHN • 1 sh; stn DW4556; MNHN • 2 sh; stn DW4572; MNHN.

### Additional material examined (not included in the description)

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4555; MNHN.

### Emended description

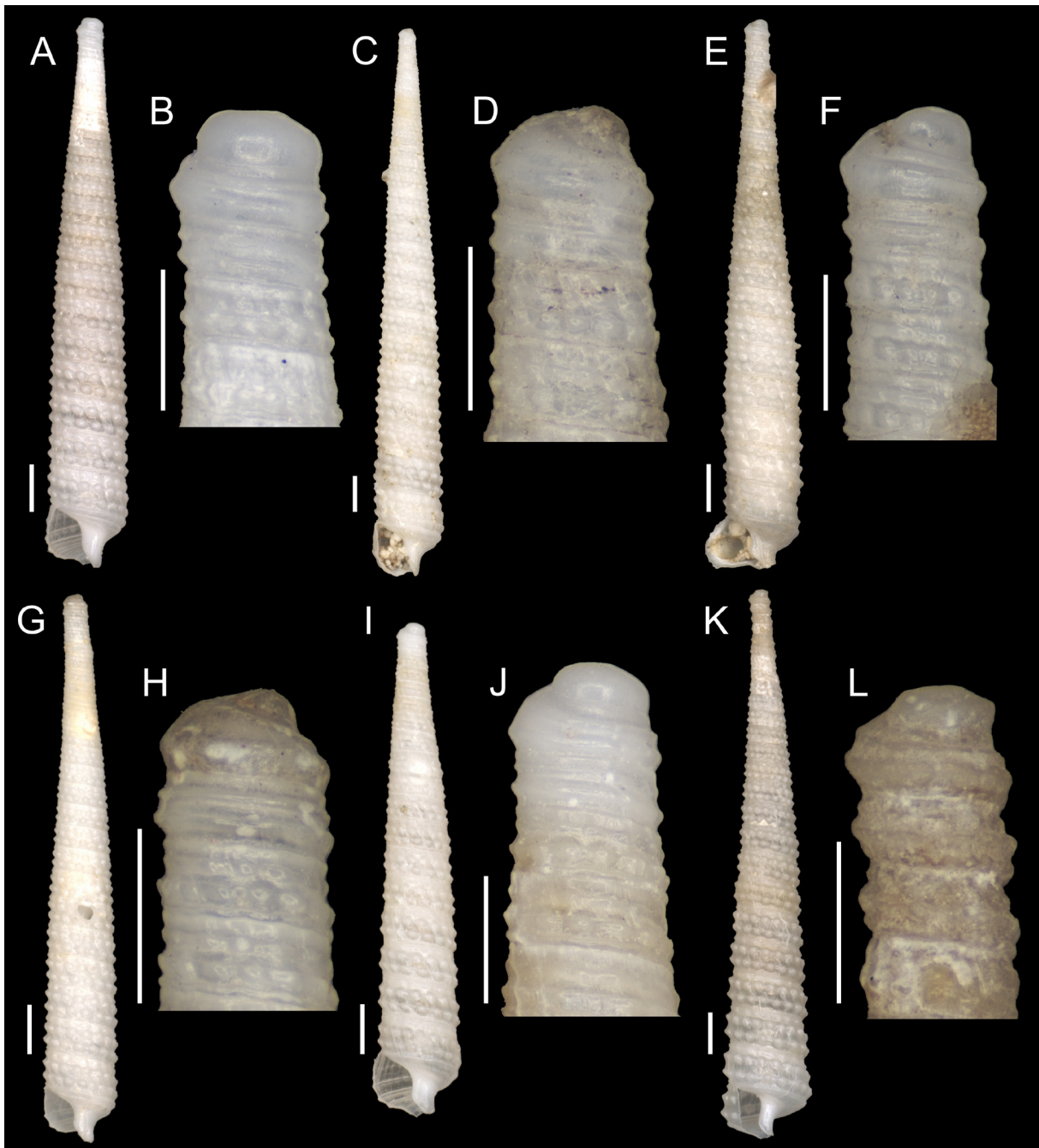
Shell sinistral, conical-fusiform, sometimes with apex constricted, up to 15.3 mm long (adult shells reach at least 9.9 mm in length), 2.2 mm wide, length/width ratio 5.5–7.5, apical angle of early whorls ~10°. Protoconch paucispiral, sub-columnar, 2.25–2.75 whorls, 0.58–0.70 mm long, 0.53–0.62 mm wide; small nucleus rises in an adapical direction and further goes abapical in an oblique descent; first whorl often slightly inflated, with initial portion mainly smooth; two main smooth spiral cords gradually appear, situated at 27–34% and 69–73% of last whorl height, abapical cord slightly to considerably more prominent, in addition to a very narrow subsutural cord; gradual transition to teleoconch, from a smooth spiral sculpture to a nodulous one. Teleoconch with up to 25 narrow whorls; three main spiral cords (continuous to those of protoconch), abapical one often more prominent in initial whorls; median spiral cord soon reaches same size as abapical cord, but adapical spiral cord slowly strengthens along teleoconch, reaching same size as other cords only in 21<sup>th</sup>–23<sup>th</sup> whorl; suture very shallow, with a smooth sutural cord; 15–18 nearly orthocline to opisthocline axial ribs on 12<sup>th</sup> teleoconch whorl; medium-sized, nearly rounded to slightly elliptical nodules; nearly smooth subperipheral cord, with a smooth, very thin basal cord right below it; a weak supranumerical cord may form between median and abapical spiral cords; small, nearly rounded to slightly elliptical aperture, 1.04–1.13 mm long, 0.74–0.88 mm wide, length/width ratio 1.2–1.5; anterior canal very short, open, 0.22–0.29 mm long, 0.23–0.30 mm wide, length/width ratio 0.8–1.2; posterior canal as a small notch, not detached from aperture. Shell white.

### Remarks

The lectotype of *S. enopla* is composed of two fragments which are probably derived from a single shell (Fernandes & Pimenta 2019a: fig. 3x), nearly matching the ~18 teleoconch whorls counted by Dall (1927). Unfortunately, the paralectotypes illustrated by Rolán & Fernández-Garcés (2008) are currently missing (NMNH invertebrate collection website). Shells of *S. cf. enopla* from Guadeloupe sometimes have a constricted apex (Figs 7–8), which is also slightly the case in the lectotype. Similarly to the type material (Rolán & Fernández-Garcés 2008), shells of *S. cf. enopla* have a protoconch with a more developed abapical spiral cord, which remains more prominent than other spirals until the initial whorls of the teleoconch. In addition, the first protoconch whorl is slightly (but not considerably) inflated. The major difference between shells from Georgia and Guadeloupe is the strength of the adapical spiral cord of the teleoconch, which is much reduced in the former, nearly indistinct. In shells from Guadeloupe, the adapical spiral cord reaches the same size as other cords only in the 21<sup>th</sup>–23<sup>th</sup> whorl, but such an equivalence of strength seems impossible to be reached in larger shells from Georgia, judging from the lectotype. Because of the little available material from the type locality, the present identification is tentative until new material becomes available for comparison.

Another similar species to *S. cf. enopla* is *Inella pseudotortricula* Rolán & Lee, 2008 from Bermuda. These two species mainly differ by their color pattern, which is entirely white in *S. cf. enopla*, but with white whorls alternating with light brown whorls in *I. pseudotortricula* (Rolán & Fernández-Garcés

2008). The types of *Inella apexbilirata* Rolán & Fernández-Garcés, 2008, from the Bahamas, have the first protoconch whorl not inflated, but with spiral cords emerging since its beginning (whereas they gradually appear in the protoconch of *S. cf. enopla*). In addition, the types of *I. apexbilirata* are small adults, reaching only 3.5 mm in length for ~nine teleoconch whorls vs 9.9–15.3 mm for a maximum of 25 teleoconch whorls in adults of *S. cf. enopla*.



**Fig. 7.** *Strobiligera cf. enopla* (Dall, 1927). **A–B.** MNHN, stn DW4544, 11.6 mm. **C–H.** MNHN, stn DW4549, 15.3 mm, 11.5 mm, 11.1 mm. **I–J.** MNHN, stn DW4550, 9.9 mm. **K–L.** MNHN, stn DW4572, 13.2 mm. Scale bars: A, C, E, G, I, K = 1 mm; B, D, F, H, J, L = 500  $\mu$ m.



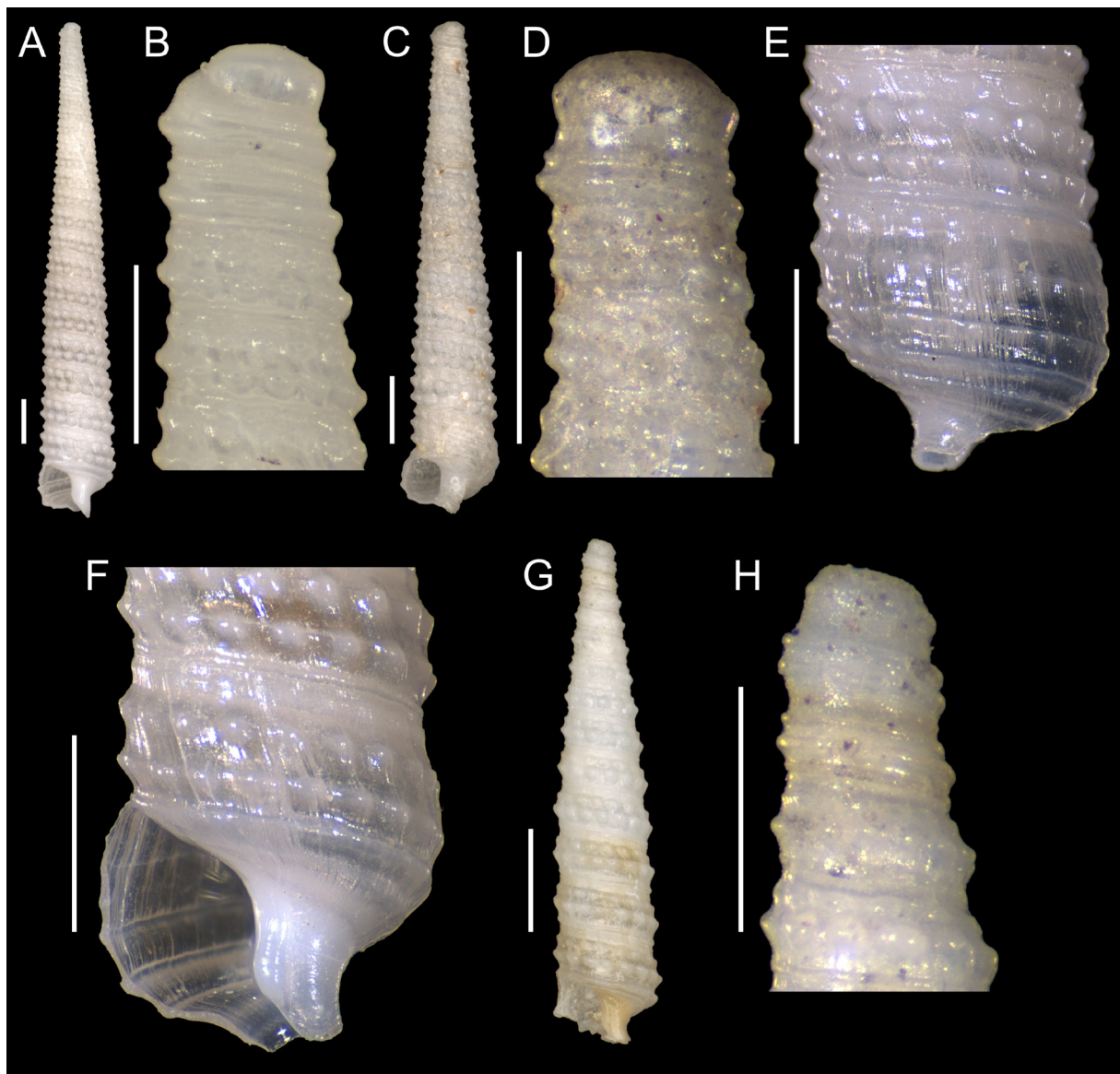
A peculiar shell from Guadeloupe (Fig. 8G–H) has reduced adapical and median spiral cords on the teleoconch when compared to typical shells of *S. cf. enopla* with the same number of teleoconch whorls, in addition to more convex whorls and cream patches along the teleoconch. I am undecided whether this is simply an atypical shell or a distinct species.

**Geographic distribution**

USA: Georgia (Dall 1927); Cuba (Rolán & Fernández-Garcés 2008); Guadeloupe (this study).

**Bathymetric distribution**

Empty shells previously known from 538–823 m (Rolán & Fernández-Garcés 2008). This study: 343–482 m (empty shells), 100–258 m (live specimen).



**Fig. 8.** *Strobiligera cf. enopla* (Dall, 1927). **A–B.** MNHN, stn DW4555, 11.1 mm. **C–D.** MNHN, stn DW4556, 7.3 mm. **E.** MNHN, stn DW4544 (same shell as Fig. 7A). **F.** MNHN, stn DW4550 (same shell as Fig. 7I). **G–H.** MNHN, stn DW4555, 4.9 mm. Scale bars: A, C, E–G = 1 mm; B, D, H = 500  $\mu$ m.

*Strobiligera picta* sp. nov.

[urn:lsid:zoobank.org:act:124616F8-440A-4554-8AC3-0A4921BD84C7](https://zoobank.org/urn:lsid:zoobank.org:act:124616F8-440A-4554-8AC3-0A4921BD84C7)

Fig. 9

**Diagnosis**

A species of *Strobiligera* with a brown band in the adapical spiral cord of the teleoconch.

**Etymology**

Latin, ‘*pictus*’ = ‘painted’. The specific name alludes to the brown band on the adapical spiral cord of the teleoconch, unusual for a deep-sea triphorid species.

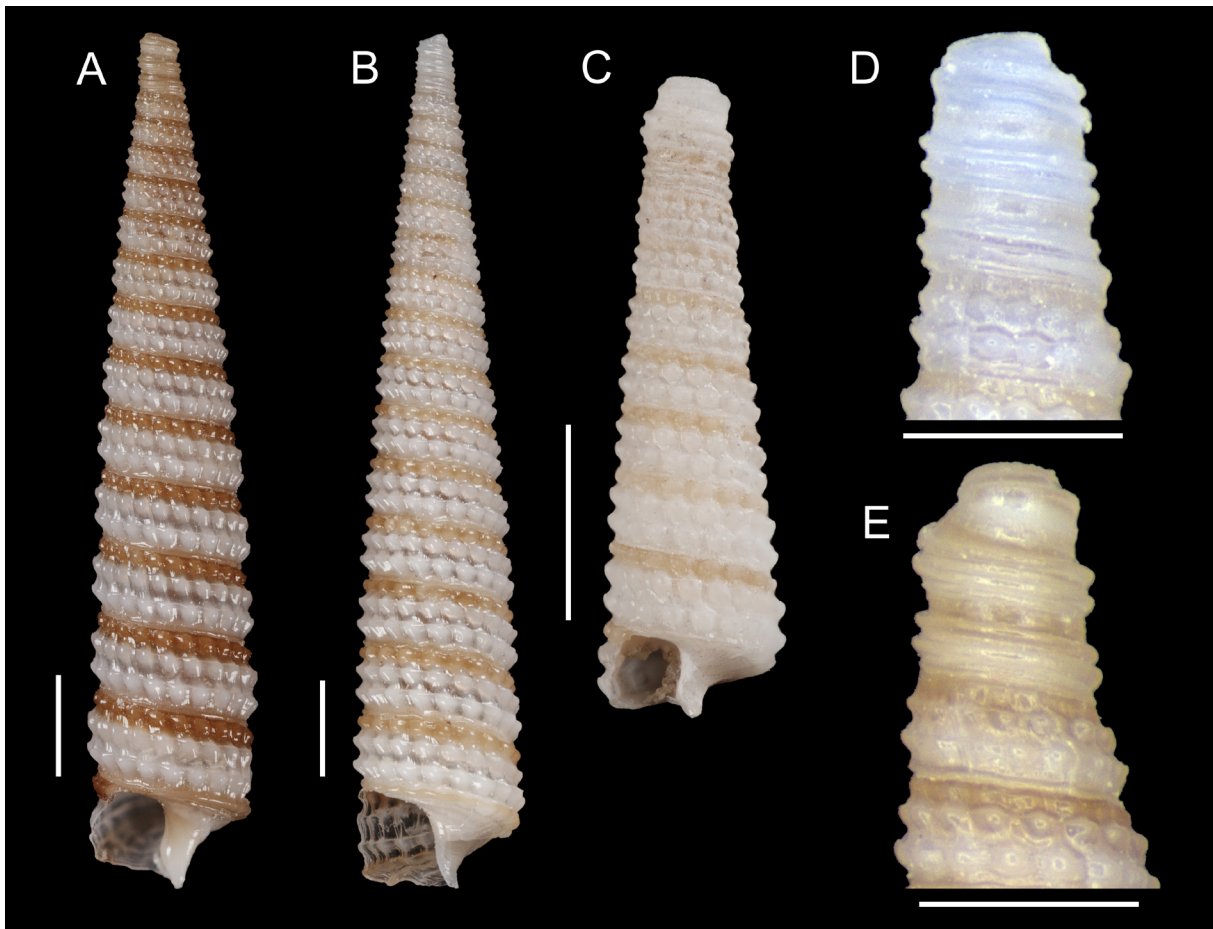
**Type material**

**Holotype**

GUADELOUPE (Karubenthos 2 expedition) • sh; stn DW4635; MNHN-IM-2000-38781.

**Paratypes**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4634; MNHN-IM-2000-38782 • 1 sh; stn DW4635; MNHN-IM-2000-38783.



**Fig. 9.** *Strobiligera picta* sp. nov. **A, E.** Holotype, MNHN-IM-2000-38781, 8.4 mm. **B, D.** Paratype, MNHN-IM-2000-38783, 8.9 mm. **C.** Paratype, MNHN-IM-2000-38782, 3.3 mm. Scale bars: A–C = 1 mm; D–E = 500  $\mu$ m.

**Type locality**

Guadeloupe, 15°50' N, 61°26' W, 265–268 m depth.

**Description**

Shell sinistral, conical-fusiform, up to 8.9 mm long (incomplete base), 1.8 mm wide, length/width ratio 4.8–4.9, apical angle of early whorls 13–17°. Protoconch paucispiral, sub-columnar, 2.75–3.5 whorls, 0.60–0.69 mm long, 0.47 mm wide; small nucleus rises in an adapical direction and further goes abapical in an oblique descent; two smooth, wide spiral cords of equal size, situated at 42–45% and 72–73% of last whorl height, in addition to a very narrow subsutural cord; gradual transition to teleoconch, from a smooth spiral sculpture to a nodulous one. Teleoconch with up to 15 whorls; three main spiral cords, two of them (median and abapical) stronger at beginning and continuous to those of protoconch, adapical spiral cord initially narrow but gradually strengthening along teleoconch, reaching same size as other cords in 13<sup>th</sup> or 14<sup>th</sup> whorl (but with a similar size since eighth whorl); suture shallow, with a smooth to slightly wavy sutural cord; 19–22 slightly opisthocline axial ribs on tenth teleoconch whorl; medium-sized, nearly rounded to slightly elliptical nodules; slightly nodulous subperipheral cord, with a smooth, very thin basal cord right below it. Shell white, with a brown (or light brown) band on adapical spiral cord and on subperipheral and basal cords, sometimes with protoconch slightly brownish.

**Remarks**

In addition to the obvious difference in shell color, *Strobiligera picta* sp. nov. is differentiated from *S. cf. enopla* by its non-inflated protoconch, its spiral cords of nearly the same strength and the adapical spiral cord of teleoconch reaching the same size as other cords in the 13<sup>th</sup>–14<sup>th</sup> whorl in *S. picta*, but only in the 21<sup>th</sup>–23<sup>th</sup> in *S. cf. enopla*. Unfortunately, the incomplete base of *S. picta* precluded further comparisons.

The most similar shells to *S. picta* sp. nov. are the Brazilian records of *I. apexbilirata* and *Inella* sp. 1 (Fernandes & Pimenta 2019a), which, however, have a different color pattern. The Brazilian shells are from the lower continental shelf (69–163 m for *I. apexbilirata*; 65–80 m for *Inella* sp. 1), whereas *S. picta* is recorded from 265–310 m and it was absent from the expedition Karubenthos 1, conducted in the shallow waters of Guadeloupe. The Brazilian record of *I. apexbilirata* is here described as a new species (see below).

**Geographic distribution**

Guadeloupe.

**Bathymetric distribution**

265–310 m (empty shells).

*Strobiligera* sp. A

Fig. 10

**Material examined**

GADELOUPE (Karubenthos 2 expedition) • 1 sh; stn CP4513; MNHN • 1 sh; stn DW4549; MNHN • 1 sh; stn DW4550; MNHN • 1 sh; stn DW4599; MNHN.

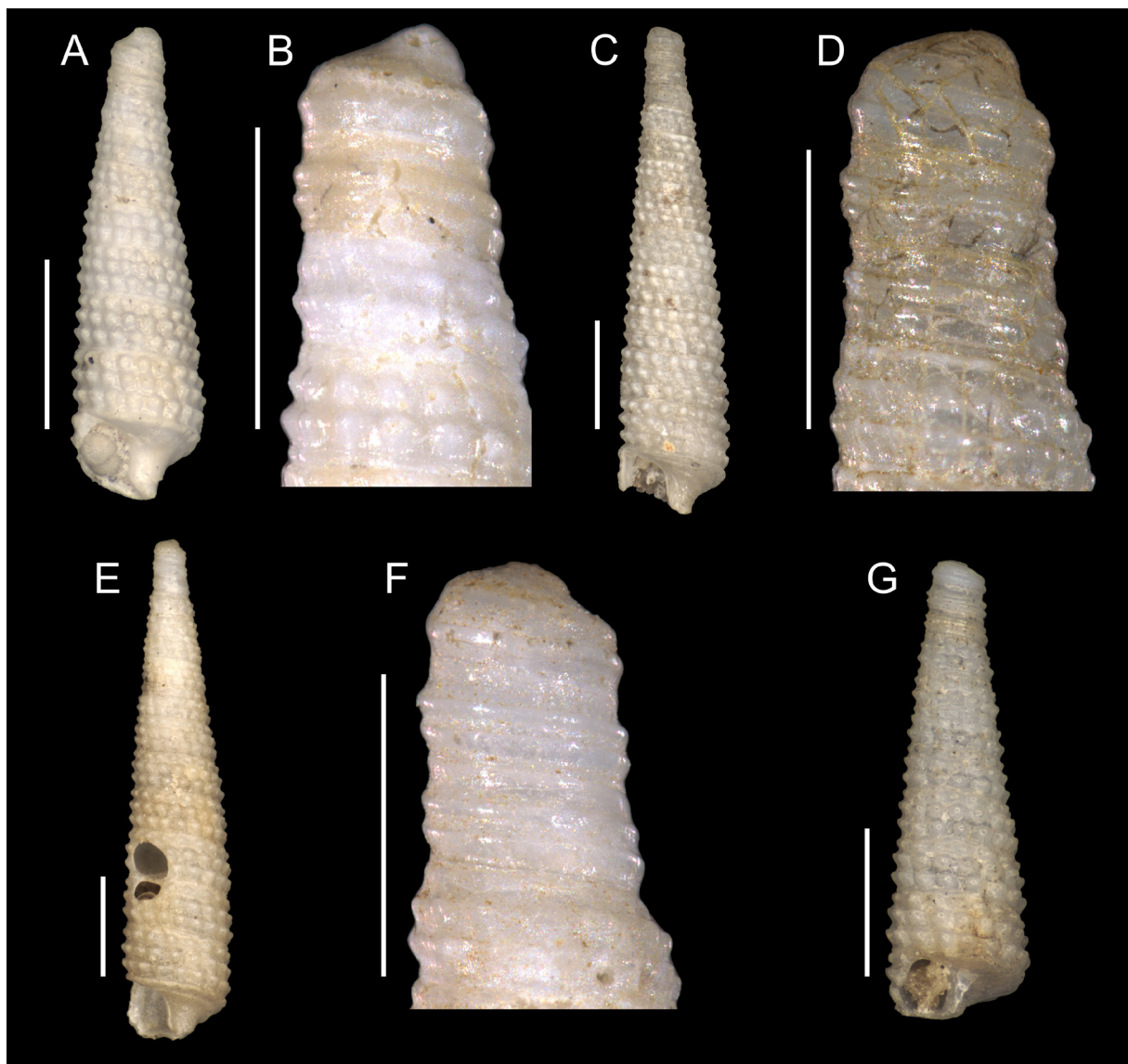
**Description**

Shell sinistral, conical-fusiform, up to 5.0 mm long, 1.1 mm wide, apical angle of early whorls 14–15°. Protoconch paucispiral, sub-columnar, 3.0–3.25 whorls, 0.59–0.73 mm long, 0.38–0.47 mm wide; small nucleus rises in an adapical direction and further goes abapical in an oblique descent; two main smooth spiral cords, similarly-sized, situated at 37–44% and 71–77% of last whorl height, in addition to a very

narrow subsutural cord; gradual transition to teleoconch, from a smooth spiral sculpture to a nodulous one. Teleoconch with up to 11 whorls; three main spiral cords (continuous to those of protoconch), adapical one initially strongly reduced, gradually strengthening and reaching same size as other cords between sixth and eighth whorls; suture shallow, with a very thin sutural cord; 18 orthocline to slightly opisthocline axial ribs on ninth teleoconch whorl; medium-sized, nearly rounded to slightly elliptical nodules; base apparently not fully developed. Shell white.

### Remarks

*Strobiligera* sp. A is currently known from small and often worn shells, of up to 5.0 mm in length, although it is uncertain whether the largest shell (Fig. 10E) is adult or juvenile. It differs from *S. cf. enopla* in the earlier full development of the adapical spiral cord of the teleoconch and in the first protoconch whorl (not slightly inflated, as observed in most shells of *S. cf. enopla*). The shell of *Strobiligera* sp. A is



**Fig. 10.** *Strobiligera* sp. A. **A–B.** MNHN, stn CP4513, 2.8 mm. **C–D.** MNHN, stn DW4549, 4.5 mm. **E–F.** MNHN, stn DW4550, 5.0 mm. **G.** MNHN, stn DW4599, 3.1 mm. Scale bars: A, C, E, G = 1 mm; B, D, F = 500  $\mu$ m.

completely white, contrasting with the brown adapical spiral cord in the teleoconch of *S. picta* sp. nov. Adult shells are required to confirm this as a new species.

### Geographic distribution

Guadeloupe.

### Bathymetric distribution

262–644 m (empty shells).

*Strobiligera variabilis* sp. nov.

[urn:lsid:zoobank.org:act:56F72111-A572-400C-80ED-DCDB2748CBE2](https://doi.org/10.5281/zenodo.10000000)

Fig. 11

*Triphora* sp. 2 – Lamy & Pointier 2018: 289, pl. 92 fig. 13.

### Diagnosis

Protoconch with a small nucleus; teleoconch with an initially weak adapical spiral cord, often reaching same size as other spiral cords between the fifth and seventh whorls.

### Etymology

Latin, ‘*variabilis*’ = ‘variable’. The specific epithet alludes to the morphological variation in the shells of this species.

### Type material

#### Holotype

GUADELOUPE (Karubenthos 2 expedition) • sh; stn DW4634; MNHN-IM-2000-38784.

#### Paratypes

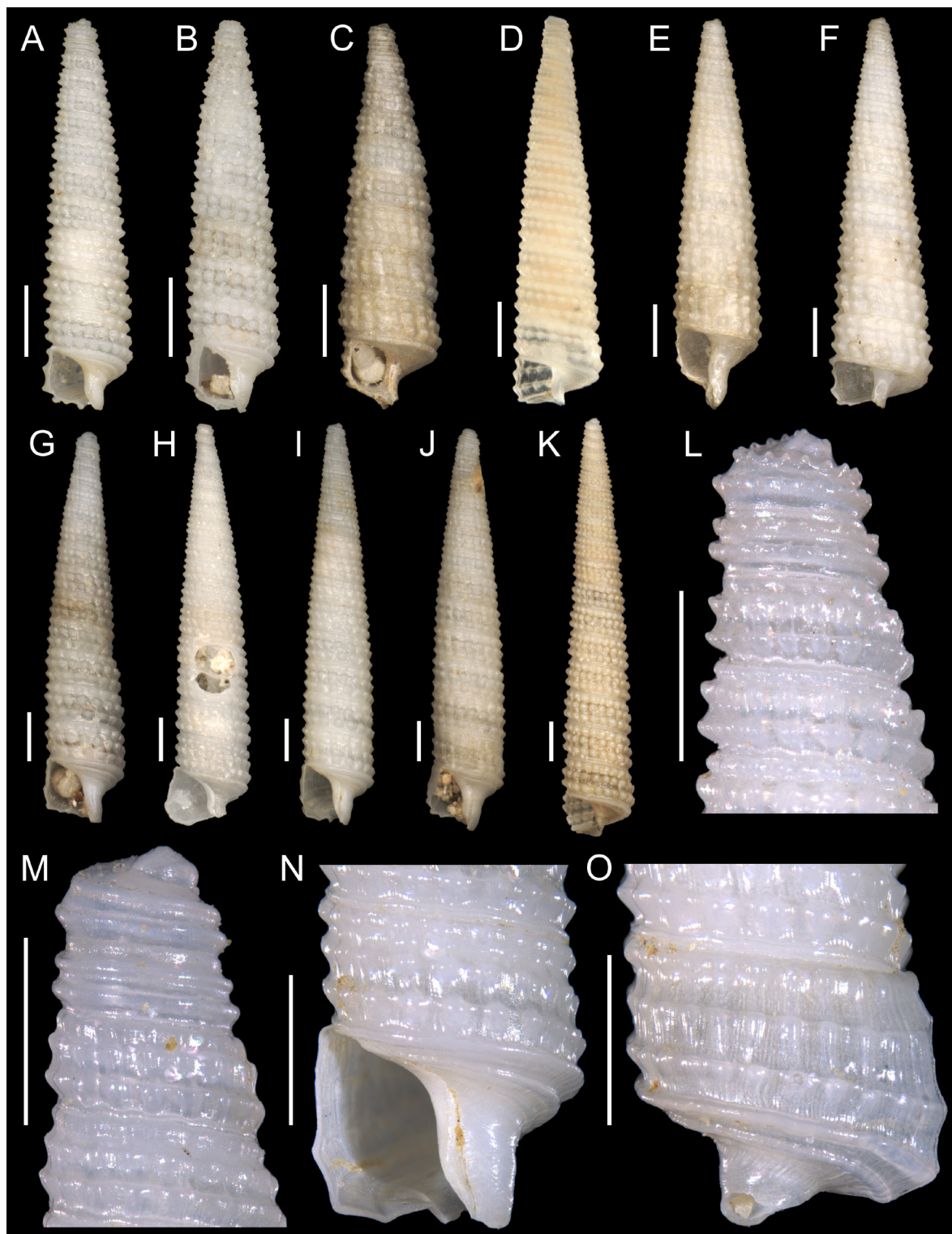
GUADELOUPE (Karubenthos 2 expedition) • 2 sh; stn DW4536; MNHN-IM-2000-38785 • 1 sh; stn DW4538; MNHN-IM-2000-38786 • 1 sh; stn DW4572; MNHN-IM-2000-38787 • 2 sh; stn DW4600; MNHN-IM-2000-38788 • 17 sh; stn DW4634; MNHN-IM-2000-38792 • 1 spec. stored in ethanol; stn DW4634; MNHN-IM-2019-20013 • 1 sh; stn DW4635; MNHN-IM-2000-38789 • 6 sh; stn DW4638; MNHN-IM-2000-38790 • 2 sh; stn DW4646; MNHN-IM-2000-38791.

### Type locality

Guadeloupe, 15°48' N, 61°26' W, 304–310 m depth.

### Description

Shell sinistral, conical-fusiform, rarely with apex slightly constricted, up to 11.0 mm long (incomplete shell; adult shells reach at least 5.0 mm in length), 2.0 mm wide, length/width ratio 4.1–5.6, apical angle of early whorls 16–18°. Protoconch paucispiral, sub-columnar, 2.0–3.0 whorls, often 0.44–0.52 mm long (one discrepant protoconch up to 0.65 mm long), 0.50–0.61 mm wide; small nucleus rises in an adapical direction and further goes abapical in an oblique descent; two main spiral cords (in addition to a very narrow subsutural cord), situated at 32–36% and 72–75 % of last whorl height and often smooth, but both cords may have some degree of nodules (especially adapical one, which may show pointed, triangular nodules, resembling a thorn crown); gradual transition to teleoconch, from an often smooth spiral sculpture to a nodulous one. Teleoconch with up to 16 whorls; three main spiral cords (continuous with those of protoconch), adapical one initially reduced, gradually strengthening and may reach nearly same size as other cords between fifth and seventh whorls, or occasionally not reaching



**Fig. 11.** *Strobiligera variabilis* sp. nov. **A, L.** Holotype, MNHN-IM-2000-38784, 5.5 mm. **B.** Paratype, MNHN-IM-2000-38786, 5.0 mm. **C.** Paratype, MNHN-IM-2000-38787, 5.4 mm. **D.** Paratype, MNHN-IM-2019-20013, 7.1 mm. **E–F.** Paratypes, MNHN-IM-2000-38785, 7.4 mm, 8.0 mm. **G, I–J, M–O.** Paratypes, MNHN-IM-2000-38792 (M–N, same shell as Fig. H), 7.9 mm, 9.5 mm, 10.0 mm. **H.** Paratype, MNHN-IM-2000-38788, 9.2 mm. **K.** Paratype, MNHN-IM-2000-38789, 10.5 mm. Scale bars: A–K, N–O = 1 mm; L–M = 500  $\mu$ m.

same size as other cords until body whorl; suture very shallow, nearly indistinct, with a narrow sutural cord; 17–23 nearly orthocone axial ribs on 12<sup>th</sup> teleoconch whorl; medium-sized, rounded to slightly elliptical nodules; smooth, broad subperipheral cord, with a smooth, narrow basal cord right below it; a very weak supranumerical cord may form (or not) between median and abapical spiral cords; slightly elliptical aperture, 0.76–1.25 mm long, 0.51–0.85 mm wide, length/width ratio 1.5; anterior canal very short, often open, 0.14–0.22 mm long, 0.22–0.31 mm wide, length/width ratio 0.6–0.7. Shell white to dirty-white.

### Remarks

Shells of *Strobiligera variabilis* sp. nov. are highly variable with respect to length (there are small adults – Fig. 11A, and large immatures – Fig. 11K), width, sculpture of spiral cords of protoconch (smooth to slightly nodulous), strength of the adapical spiral cord of the teleoconch, and number of axial ribs. However, variation is often continuous, and it is hard to define whether more than one species is involved with only empty shells at hand (only one live specimen was sampled, and the head-foot was used for DNA extraction – unpubl. data). Until compelling evidence indicates otherwise, I conservatively consider this as a single (but variable) species. The holotype is a small adult shell (Fig. 11A) with slightly nodulous spiral cords on the protoconch (Fig. 11L).

The most similar species to *S. variabilis* sp. nov. is *Strobiligera* sp. A (Fig. 10), which seems smaller when comparing shells with the same number of teleoconch whorls, has a narrower protoconch (0.38–0.47 mm wide vs 0.50–0.61 mm in *S. variabilis*), and a shallower suture. A deep-sea species from Georgia (USA) with a similar teleoconch morphology to *S. variabilis* is *Strobiligera meteora* (Dall, 1927), which in contrast has an inflated first protoconch whorl (Rolán & Fernández-Garcés 2008).

A slightly similar species is *Strobiligera compsa* (Dall, 1927) from Georgia (USA). Its type material consists of two shells without protoconch and base (Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2019a), precluding further comparisons. Some shells of *S. variabilis* sp. nov. (e.g., Fig. 11C) have a similar shape to these types, but the adapical spiral cord of the teleoconch in *S. variabilis* is often more developed. In addition, shells of *S. variabilis* are narrower, with the largest one reaching 11.0 mm in length and 2.0 mm in width for 14.5 teleoconch whorls vs 12 mm in length and 3.3 mm in width for 13 teleoconch whorls in *S. compsa* (based on the counting of whorls in the lectotype, not the 12 whorls described by Dall 1927).

*Strobiligera variabilis* sp. nov. is similar to *S. cf. enopla* from Guadeloupe, but the two species are distinguished by the shell shape (*S. variabilis* is broader, with the apical angle of early whorls 16–18° vs ~10° in *S. cf. enopla*), the strength of the adapical spiral cord of the teleoconch (often reaching nearly the same size as other cords between the fifth and seventh whorls in *S. variabilis*, vs only in the 21<sup>th</sup>–23<sup>th</sup> whorl in *S. cf. enopla*) and the strength of the median spiral cord on the initial whorls of the teleoconch (with the same size of abapical cord in *S. variabilis*, vs often more reduced than the abapical cord in *S. cf. enopla*). The protoconch of *S. variabilis* sometimes has nodules on the spiral cords (especially the adapical one), which is not observed in *S. cf. enopla*; on the other hand, the first protoconch whorl of *S. cf. enopla* is often slightly inflated (but never inflated in *S. variabilis*). The Bahamian species *Inella apexbilarata* Rolán & Fernández-Garcés, 2008 has one protoconch whorl more than *S. variabilis*, in addition to a much weaker adapical spiral cord on the teleoconch.

The complex taxonomic situation of “*Inella*” *triserialis* (Dall, 1881) [and to a lesser extent of “*Inella*” *intermedia* (Dall, 1881)] is carefully explained here in order to avoid further confusion. I complement the observations of Fernandes & Pimenta (2019a: 7), who corrected the lectotype designation of “*I.*” *intermedia* because the previous designation by Rolán & Fernández-Garcés (2008): (1) erroneously considered a wide range for the type locality of “*I.*” *intermedia* [although Dall (1881) mentioned

only “station 2, 805 fms”]; (2) ignored the MCZ labels and annotations in the catalogue book [which indicated MCZ 7382 and MCZ 7384 as syntypes of “*I.*” *triserialis*, as observed but not followed in Rolán & Fernández-Garcés (2008: caption of fig.14g–h)]; (3) and followed the subsequent drawing of Dall (1889a) for the choice of lectotype [although the shell in MCZ 7384, with 13 teleoconch whorls, does not match the drawing of “*I.*” *intermedia*, with 17 teleoconch whorls]. Dall (1881) stated for “*I.*” *intermedia* that the ‘specimen measured is the most perfect, but not the largest’; it was 11.0 mm long and smaller than the lectotype designated by Fernandes & Pimenta (2019a), which was 12.6 mm long for ~19 teleoconch whorls [i.e., less than the largest shell, with about 23 whorls (Dall 1881)]. Because the lectotype is worn, it is possible that the shell illustrated in Dall (1889a) would be the ‘most perfect’, and has not been photographed yet. Apart of that, “*I.*” *intermedia* and the paralectotypes MCZ 7382 and MCZ 7384 of “*I.*” *triserialis* are possibly conspecific with “*I.*” *longissima*, thus requiring the examination of more material. The type material of “*I.*” *triserialis* stored in the NMNH collection (lectotype and one paralectotype) seems different, apparently with a much earlier emergence of the median spiral cord of the teleoconch (Rolán & Fernández-Garcés 2008), and it possibly includes a shell illustrated by Dall (1889a: fig. 5a), despite the broken apex. However, as also recognized by Rolán & Fernández-Garcés (2008), the other shell illustrated by Dall (1889a: fig. 6a) as “*I.*” *triserialis* is another species, much longer and apparently with the adapical spiral cord weaker on the initial whorls of the teleoconch (although this is hardly visible in the drawing). This shell has no precise locality, and it seems very similar to some shells of *S. variabilis* sp. nov. (e.g., Fig. 11K), albeit slightly longer (15.5 mm vs 11.0 mm in an incomplete shell of *S. variabilis*). More material is required in order to check the geographic range of *S. variabilis*.

#### **Geographic distribution**

Guadeloupe (Lamy & Pointier 2018; this study).

#### **Bathymetric distribution**

Empty shells previously known from 200 m (Lamy & Pointier 2018, determined as *Triphora* sp. 2). This study: 250–680 m (empty shells), 304–310 m (live specimen).

#### ***Strobiliger* cf. *compsa* (Dall, 1927)**

Fig. 12

*Triphora (Strobiliger) compsa* Dall, 1927: 96.

*Triphora (Strobiliger) compsa* – Abbott 1974: 112, fig. 1154.

*Inella compsa* – Rolán & Fernández-Garcés 2008: 118, fig. 17f–g.

*Strobiliger compsa* – Fernandes & Pimenta 2014: 169; 2019a: fig. 3r.

#### **Type material**

##### **Lectotype**

USA • sh; off Georgia; 805 m depth; USNM 333518.

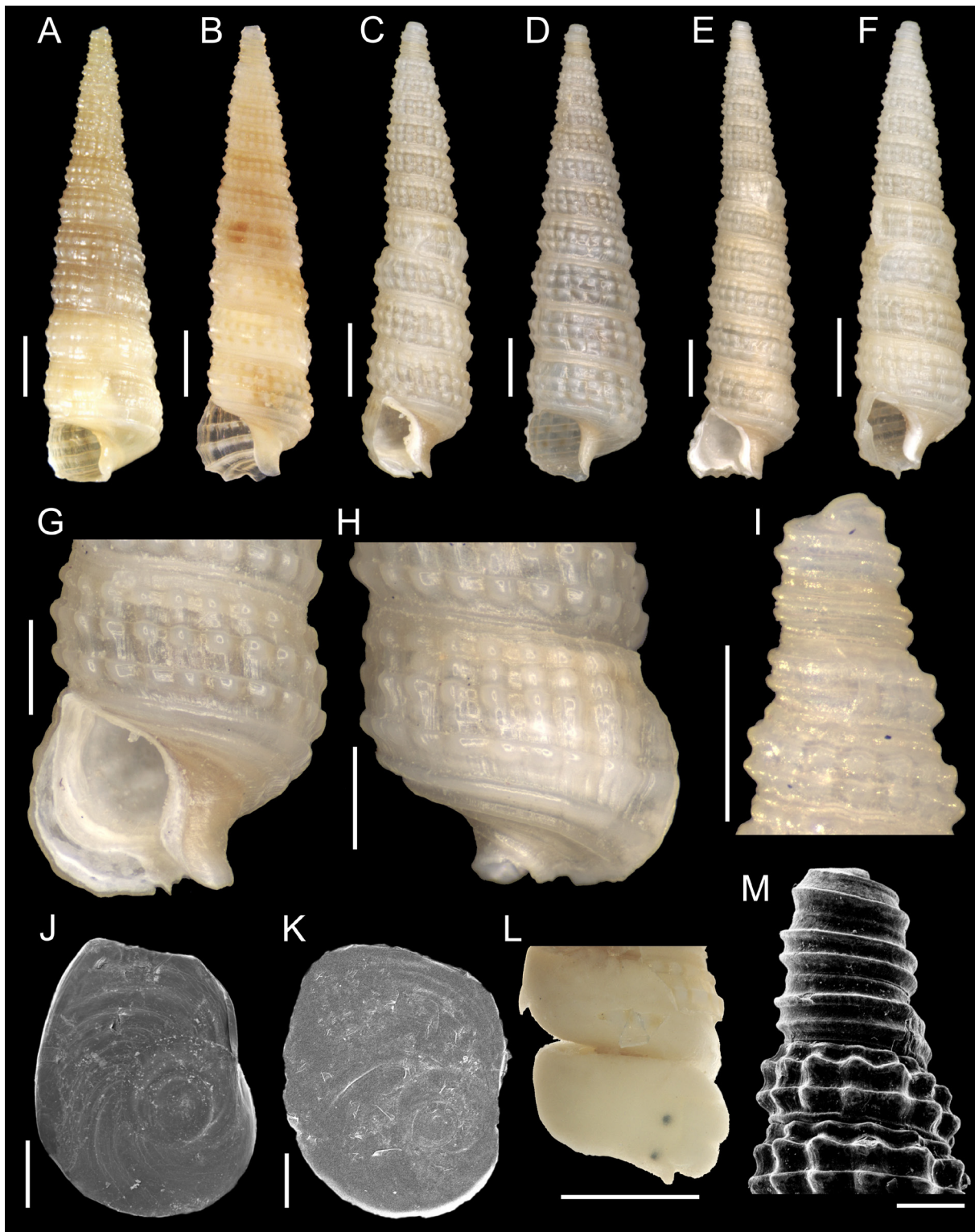
##### **Paralectotype**

USA • 1 sh; same locality as for lectotype; USNM 1592924.

#### **Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4572; MNHN • 25 sh, 3 specs stored dry; stn DW4646; MNHN • 2 specs stored in ethanol; same data as for preceding; MNHN-IM-2019-20014.





**Fig. 12.** *Strobiligera* cf. *compsa* (Dall, 1927). A–B, J–M. MNHN-IM-2019-20014, stn DW4646 (K–L from shell A; J, M from shell B), 7.6 mm, 6.9 mm. C–I. MNHN, stn DW4646 (G–I from shell C), 6.2 mm, 7.8 mm, 8.1 mm, 5.8 mm. Scale bars: A–F, L = 1 mm; G–I = 500  $\mu$ m; J–K, M = 200  $\mu$ m.

### Emended description

Shell sinistral, conical, up to 8.1 mm long (adult shells reach at least 5.8 mm in length), 2.1 mm wide, length/width ratio 3.7–4.7, apical angle of early whorls 19–24°; some shells show a distinct change in width on seventh teleoconch whorl or after (indicated by a scar), becoming broader, whereas others maintain their width; additional scars may appear in late whorls, after which teleoconch sculpture may become smooth, polished. Protoconch paucispiral, truncated, 2.5–3.0 whorls, 0.44–0.59 mm long, 0.43–0.54 mm wide; small nucleus rises in an adapical direction and further goes abapical in an oblique descent; two smooth, wide spiral cords of equal size, situated at 34–37% and ~69% of last whorl height, in addition to a narrow subsutural cord; transition to teleoconch demarcated by a thin scar in some shells, but not discernible in others. Teleoconch with up to 12 whorls; three main spiral cords (continuous to those of protoconch), two of them (median and abapical) stronger at beginning, adapical spiral cord initially narrow but gradually strengthening along teleoconch, reaching nearly same size as other cords between sixth and ninth whorls; suture distinct, with a smooth sutural cord; 22–25 nearly orthocline axial ribs on eighth teleoconch whorl; moderately large, nearly rounded nodules; wide, smooth subperipheral cord, two smooth basal cords (adapical one prominent, abapical narrow); two supranumerical cords appear in some shells, one between adapical and median cords, another between median and abapical cords; oval, broad aperture, 0.87–1.19 mm long, 0.62–0.88 mm wide, length/width ratio 1.0–1.4; open, very short anterior canal, 0.17–0.38 mm long, 0.26–0.31 mm wide, length/width ratio 0.6–1.4; posterior sinus very small. Shell white. Operculum elliptical, moderately thin but rigid, semi-transparent, up to 3.5 distinct whorls, nucleus slightly eccentric, dislocated 34–43% from center towards margin.

### Remarks

The lectotype of *S. compsa* (figured in Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2019a) is very similar to some shells from Guadeloupe (Fig. 12A), but the absence of protoconch and base in the type material precluded comparisons. The lectotype (12 mm long and 3.3 mm wide for 13 teleoconch whorls) is slightly larger than shells from Guadeloupe (up to 8.1 mm long, 2.1 mm wide for 12 teleoconch whorls). The geographic distance of 2400 km between the type locality and Guadeloupe is also large for a non-planktotrophic species (assuming that the population from Georgia, USA has the same development mode). Therefore the present identification is tentative.

According to Fernandes & Pimenta (2019a), records of *S. compsa* from Brazil are erroneous. The records from intertidal sites in Venezuela (Nava & Severeyn 2010; Severeyn *et al.* 2017) are also incorrect, requiring images for further identification.

Another very similar species to *S. cf. compsa* from Guadeloupe is *Strobiligera torticula* (Dall, 1881), from Yucatán Strait and the Straits of Florida (Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2015b). These two species are particularly similar with respect to their shells, which show a distinct change in their width after the seventh teleoconch whorl (Fig. 12C, E–F). However, the shell of *S. torticula* is larger (up to 25 mm long for 17.5 teleoconch whorls – Rolán & Fernández-Garcés 2008) than that of *S. cf. compsa* (up to 8.1 mm long for 12 teleoconch whorls), and the protoconch of *S. torticula* is multispiral, typical of planktotrophic development (Fernandes & Pimenta 2015b), instead of the paucispiral protoconch, typical of non-planktotrophic development in *S. cf. compsa* (Fig. 12I, M).

The most similar species to *S. cf. compsa* in Guadeloupe is *S. variabilis* sp. nov., but *S. cf. compsa* has much more convex whorls, a wider body whorl and base, more widely spaced basal cords (not too close to the subperipheral cord, as in *S. variabilis*), and the spiral cords of the protoconch never show the ‘crispy’ condition (with small nodules) observed in some shells of *S. variabilis*.

**Geographic distribution**

USA: Georgia (Dall 1927); Guadeloupe (this study).

**Bathymetric distribution**

Empty shells previously known from 805 m (Dall 1927). This study: 250–399 m (empty shells), 250–254 m (live specimens).

***Strobiligera dinea* (Dall, 1927)**

Figs 13–15

*Triphora (Strobiligera) pompona* var. *dinea* Dall, 1927: 95.

*Triphora (Strobiligera) dinea* – Abbott 1974: 112.

*Inella dinea* – Rolán & Fernández-Garcés 2008: 126, fig. 19d–i.

*Strobiligera dinea* – Fernandes & Pimenta 2014: 169; 2019a: 37, figs 3u–v, 21.

**Type material****Lectotype**

USA • sh; off Georgia; USNM 333517. 11 paralectotypes are stored in the same lot.

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 2 sh; stn DW4536; MNHN • 19 sh; stn DW4549; MNHN • 2 sh, 1 spec. stored dry; stn DW4550; MNHN • 1 sh; stn DW4599; MNHN • 4 sh, 1 spec. stored dry; stn DW4634; MNHN • 1 sh; stn CP4649; MNHN.

**Emended description**

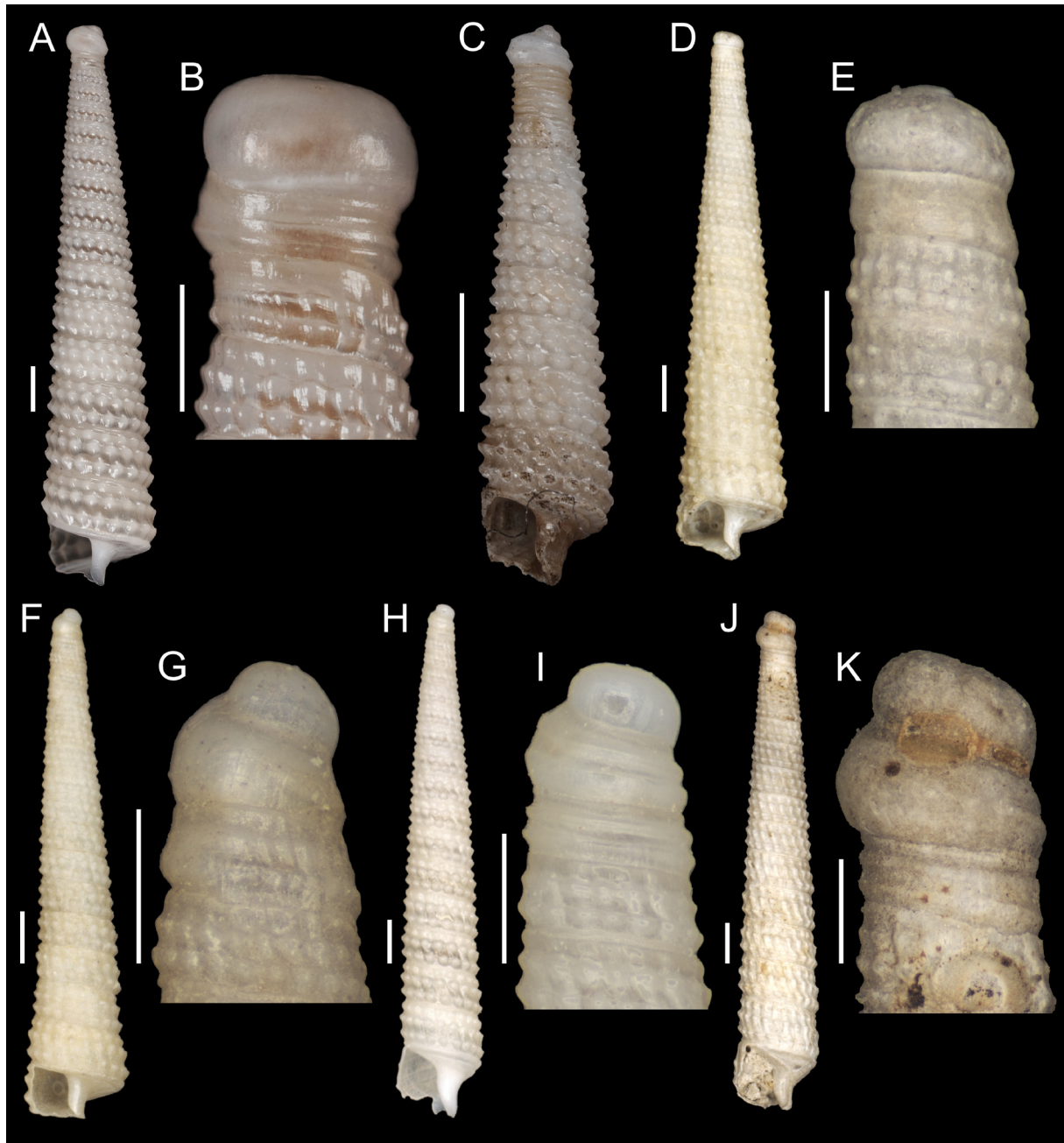
Shell sinistral, conical-fusiform, a few shells slightly constricted at apex, up to 20.1 mm long (adult shells reach at least 11.1 mm in length), 2.8 mm wide, length/width ratio 5.5–7.0, apical angle of early whorls 11–13°. Protoconch paucispiral, globose, 2.25–3.0 whorls, 0.75–1.25 mm long, 0.70–1.03 mm wide; first whorl smooth, much inflated, sometimes slightly wider (up to 1.1 ×) than last whorl; second whorl with two smooth spiral cords, situated at 32–42% and 69–72% of last whorl height, abapical cord sometimes slightly more prominent, in addition to a very narrow subsutural cord; gradual transition to teleoconch, from a smooth spiral sculpture to a nodulous one. Teleoconch with up to 21 whorls; three main spiral cords (continuous with those of protoconch), adapical one considerably reduced in initial whorls, but gradually strengthening and sometimes reaching a similar size (never equal) as other cords near body whorl; suture very shallow, almost indistinct, with a narrow sutural cord; 17–20 orthocline to slightly opisthocline axial ribs on 12<sup>th</sup> teleoconch whorl; medium-sized, nearly rounded to slightly elliptical nodules; smooth subperipheral cord, with a smooth, very thin basal cord right below it; a weak to distinct supranumerical cord may form between median and abapical spiral cords; nearly rounded to slightly elliptical aperture, 1.16–1.99 mm long, 0.89–1.42 mm wide, length/width ratio 1.2–1.4; anterior canal very short, often open (sometimes partially closed), 0.35–0.41 mm long, 0.41–0.55 mm wide, length/width ratio 0.7–0.9; posterior canal as a minute notch. Shell white.

**Remarks**

*Strobiligera dinea* has a distinctive inflated first protoconch whorl. Two other West Atlantic species share this feature: *Strobiligera inflata* (Watson, 1880) and *Strobiligera pompona* (Dall, 1927). However these two species are distinguished by their reduced adapical spiral cord on the teleoconch. Dall (1927) noted that *S. dinea* has a less prominent sculpture than *S. pompona*, but possibly this is because most types are worn; for example, intact shells from Guadeloupe have a prominent teleoconch sculpture.

Shells from Guadeloupe show considerable variation in adult length, protoconch dimensions and the development of the adapical spiral cord. One atypical shell (Fig. 13C), with 3.25 protoconch whorls (0.57 mm wide only) and a considerably developed adapical spiral cord on the teleoconch, was not included in the description because it may represent a distinct species.

The most similar species to *S. dinea* from Guadeloupe is *S. cf. enopla*, which has a less inflated first protoconch whorl, reduced protoconch dimensions (0.58–0.70 mm long, 0.53–0.62 mm wide vs 0.75–1.25 mm long, 0.70–1.03 mm wide in *S. dinea* from Guadeloupe), and its adapical spiral cord on the

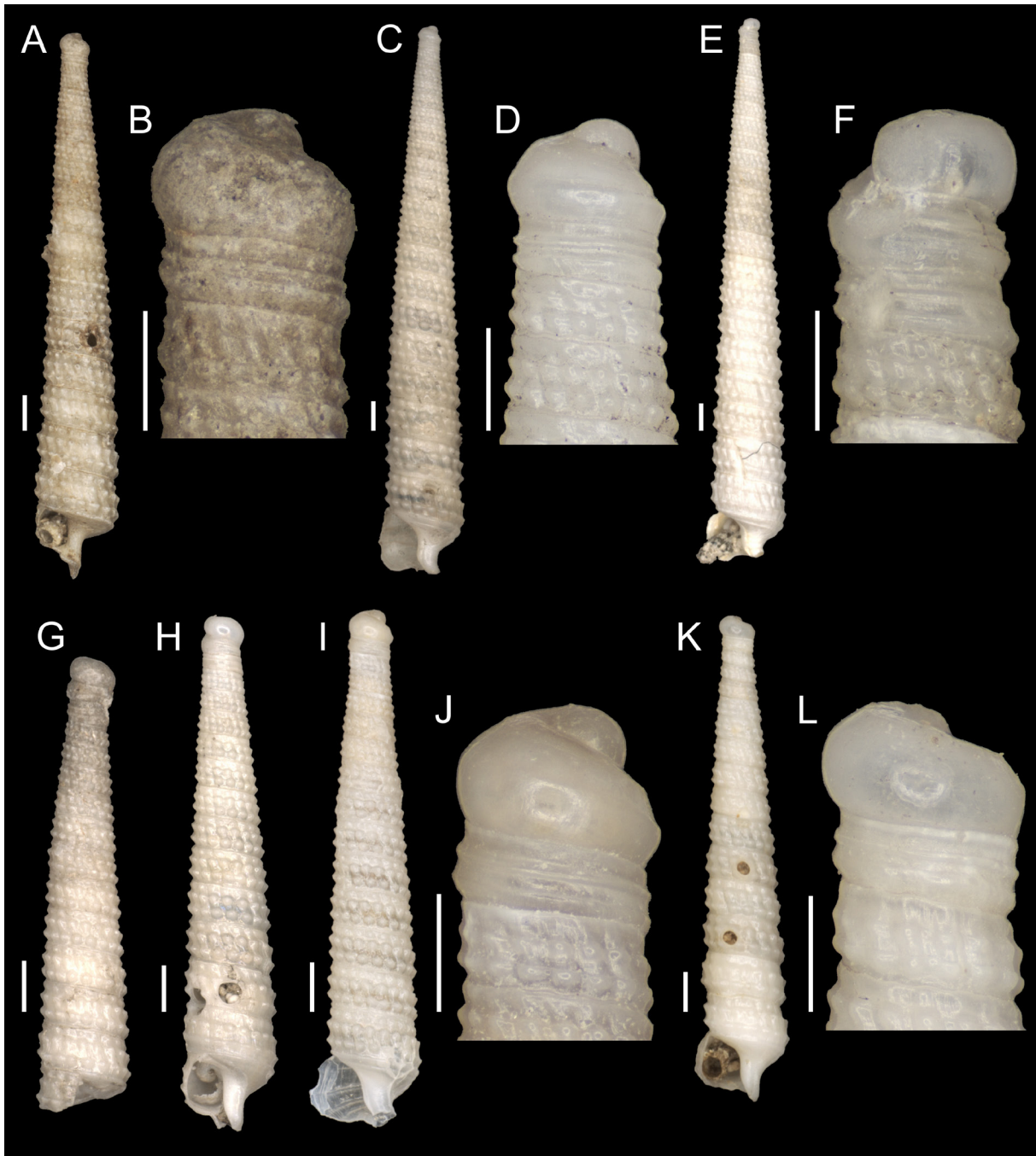


**Fig. 13.** *Strobiligera dinea* (Dall, 1927). **A–B.** MNHN, stn CP4649, 12.4 mm. **C.** MNHN, stn DW4599, 4.7 mm. **D–G.** MNHN, stn DW4536, 11.4 mm, 9.8 mm. **H–K.** MNHN, stn DW4549, 11.8 mm, 12.3 mm. Scale bars: A, C–D, F, H, J = 1 mm; B, E, G, I, K = 500  $\mu$ m.

teleoconch often develops slower than in *S. dinea*. However, sometimes it is difficult to distinguish both species.

**Geographic distribution**

USA: Georgia (Dall 1927); Guadeloupe (this study); Brazil: off Espírito Santo, Champlain Seamount (Fernandes & Pimenta 2019a).



**Fig. 14.** *Strobiligera dinea* (Dall, 1927). A–H. MNHN, stn DW4549, 15.4 mm, 18.6 mm, 20.1 mm, 8.9 mm, 11.1 mm. I–L. MNHN, stn DW4550, 10.4 mm, 12.2 mm. Scale bars: A, C, E, G–I, K = 1 mm; B, D, F, J, L = 500  $\mu$ m.

### Bathymetric distribution

Empty shells previously known from 607–940 m (Fernandes & Pimenta 2019a). This study: 262–482 m (empty shells), 304–482 m (live specimens).

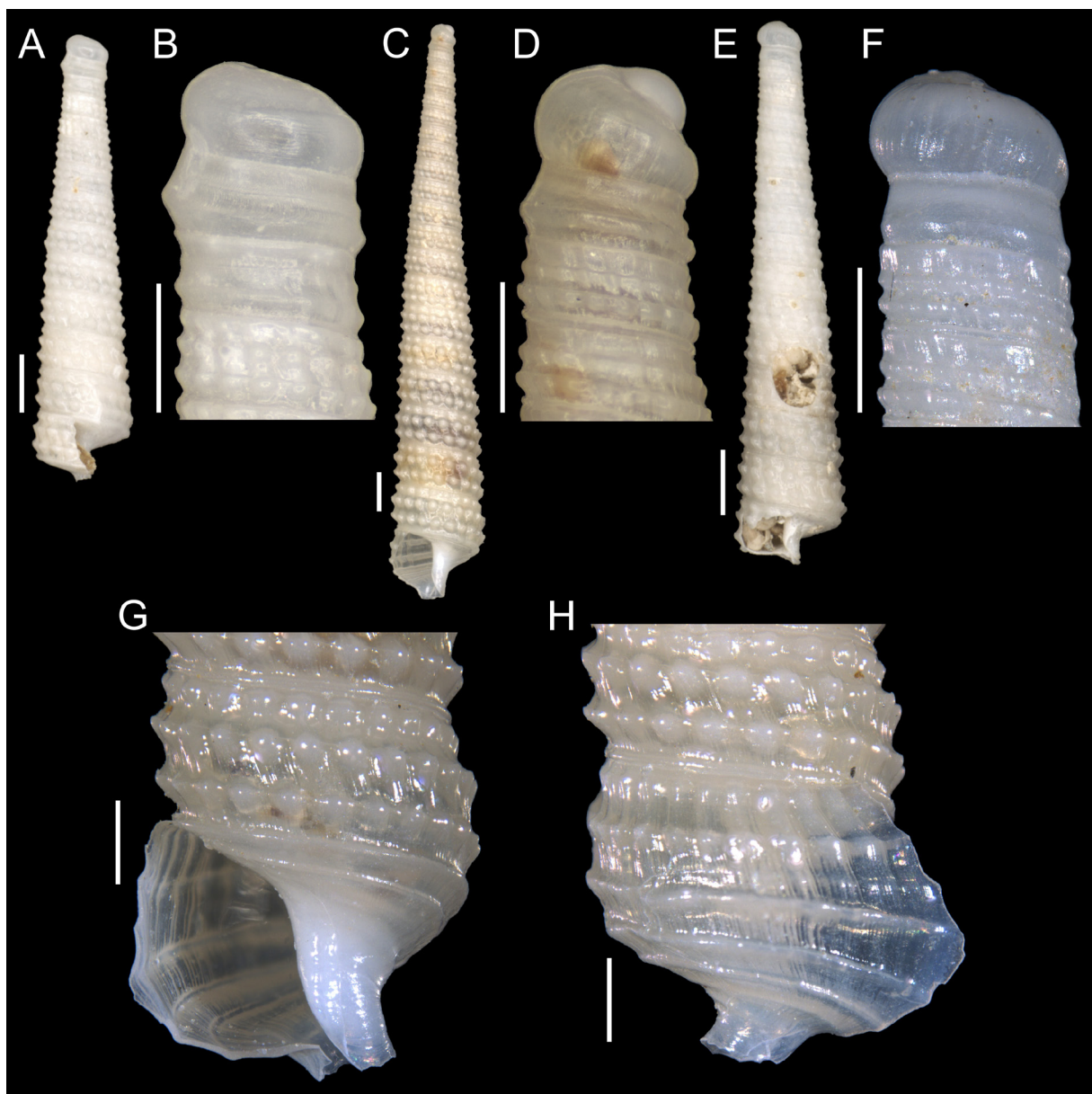
### *Strobiligera cupella* sp. nov.

[urn:lsid:zoobank.org:act:B4B076E3-B74E-4727-B5BF-9258179D56DA](https://zoobank.org/urn:lsid:zoobank.org:act:B4B076E3-B74E-4727-B5BF-9258179D56DA)

Fig. 16A–G

### Diagnosis

Elongated shell with a late adapical spiral cord on the teleoconch; protoconch beige to light brown, paucispiral, dome-shaped, mainly smooth.



**Fig. 15.** *Strobiligera dinea* (Dall, 1927). A–B. MNHN, stn DW4550, 7.7 mm. C–F. MNHN, stn DW4634, 14.7 mm, 8.3 mm. G–H. MNHN, stn DW4549. Scale bars: A, C, E = 1 mm; B, D, F–H = 500 µm.

**Etymology**

Latin, ‘*cupella*’ = ‘dome’. The specific epithet alludes to the dome-shaped first protoconch whorl of this species.

**Type material****Holotype**

GUADELOUPE (Karubenthos 2 expedition) • spec. stored dry; stn DW4554; MNHN-IM-2000-38793.

**Paratypes**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4538; MNHN-IM-2000-38794 • 1 sh; stn DW4556; MNHN-IM-2000-38795 • 2 sh; stn DW4572; MNHN-IM-2000-38796.

**Type locality**

Guadeloupe, 16°21' N, 60°56' W, 300–370 m depth.

**Description**

Shell sinistral, conical-fusiform, incomplete shells up to 15.8 mm long and 2.7 mm wide; apical angle of early whorls 12–14°. Protoconch paucispiral, 2.5–2.75 convex whorls, 0.54–0.64 mm long, 0.49–0.52 mm wide; first whorl dome-shaped, globose, mainly smooth but with few, minute pustules; subsequent whorls with two spiral cords, situated at 31–33% and 63–74% of whorl height, in addition to a much smaller subsutural cord; no axial sculpture. Teleoconch with up to 24.5 whorls (incomplete); three main spiral cords, continuous with those of protoconch; adapical spiral cord initially very narrow and gradually enlarges through teleoconch, but never reaches same size as other cords; shallow suture, almost indistinct, with a very narrow, smooth sutural cord; ~15 nearly orthocline to slightly opisthocline axial ribs on 12<sup>th</sup> whorl; medium-sized to moderately large, nearly rounded to slightly elliptical nodules; unknown base. Protoconch beige to light brown, teleoconch white to dirty-white.

**Remarks**

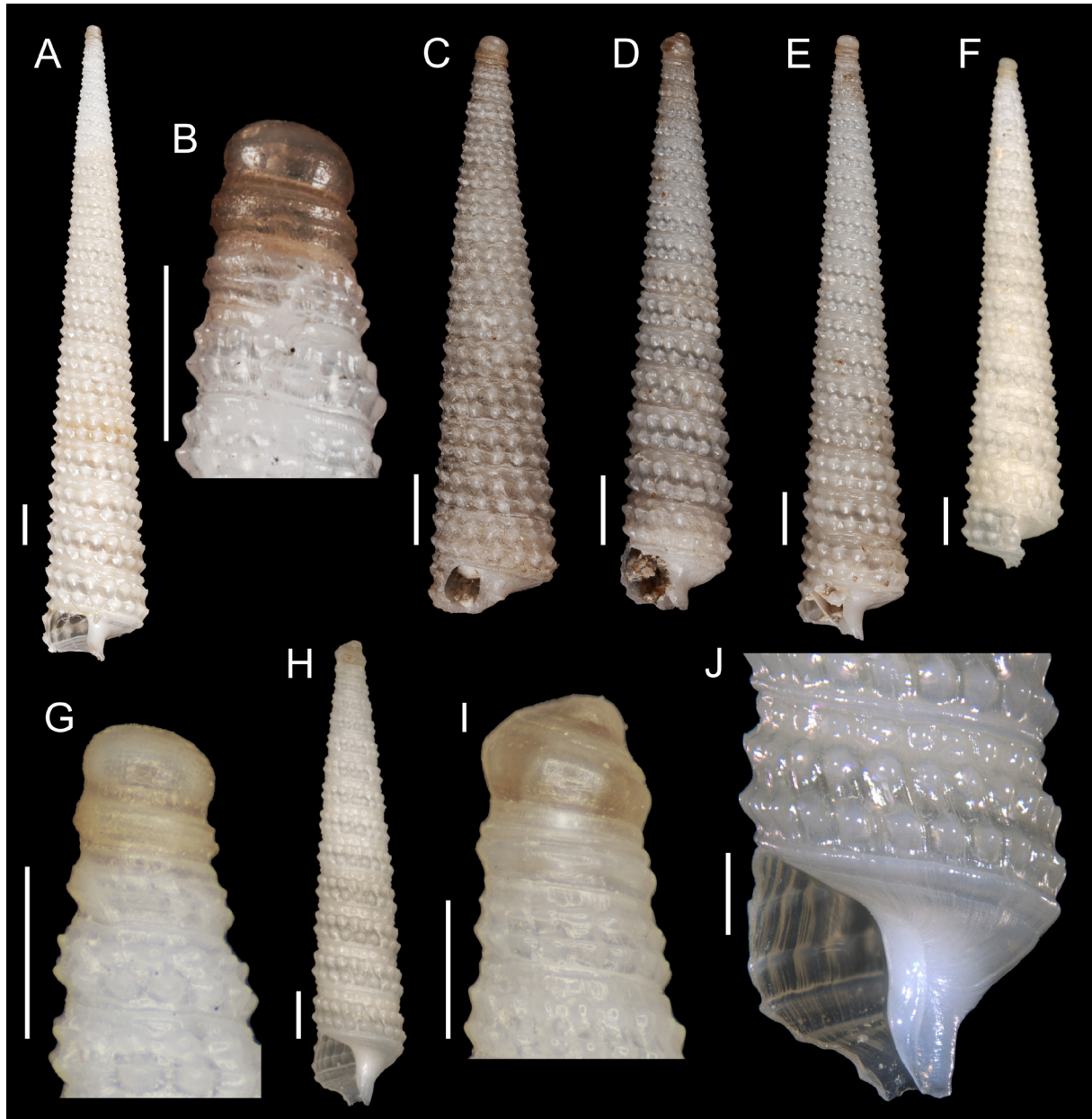
Despite the moderately long shell, no adults (with a complete base) are known of *Strobiligera cupella* sp. nov. This species differs from all other Caribbean species (Rolán & Fernández-Garcés 2008), e.g., *S. enopla* has a reduced adapical spiral cord on the teleoconch and a white protoconch with the first whorl slightly inflated and the second whorl with unequal spiral cords (the abapical one more prominent, whereas the two spiral cords are nearly equal in the beige to light brown protoconch of *S. cupella*). The colored and dome-shaped (not inflated) protoconch of *S. cupella* also distinguishes it from *S. dinea*, which has a larger protoconch (shells from Guadeloupe: 0.75–1.25 mm long, 0.70–1.03 mm wide vs 0.54–0.64 mm long, 0.49–0.52 mm wide in *S. cupella*) and a more developed adapical spiral cord on the teleoconch. *Strobiligera cupella* is differentiated from *Strobiligera colon* (Dall, 1881) comb. nov. from Cuba by the slightly more pronounced adapical spiral cord on the teleoconch (almost indistinct in *S. colon*) and the more prominent and rounded nodules of the teleoconch; the protoconch of *S. colon* is unknown (Rolán & Fernández-Garcés 2008). The paucispiral protoconch of *S. cupella* distinguishes it from the multispiral protoconch of *Strobiligera georgiana* (Dall, 1927), although the type material of the latter is worn (Rolán & Fernández-Garcés 2008).

*Strobiligera cupella* sp. nov. shares some similarities with three Brazilian species (Fernandes & Pimenta 2019a), but the absence of a complete base in the available shells of *S. cupella* precluded further comparisons. Its adapical spiral cord on the teleoconch has a similar development to that on some shells of *Strobiligera unicornium* Simone, 2006 (e.g., Fernandes & Pimenta 2019a: fig. 18a), but it develops later than on other shells (e.g., Fernandes & Pimenta 2019a: fig. 18b–c) and earlier than on others (e.g., the holotype); however, the protoconch of *S. cupella* is slightly shorter (0.54–0.64 mm long

vs 0.69–0.76 mm long in *S. unicornium*) and has a less inflated first protoconch whorl. The adapical spiral cord on the teleoconch in *S. cupella* is considerably reduced if compared to *Strobiligera campista* Fernandes & Pimenta, 2019. *Strobiligera cupella* has nodules and internodular spaces on the spiral cords of the teleoconch with the same white color, but the internodular spaces are slightly darker than the nodules in the morph named *Strobiligera* sp. 2 by Fernandes & Pimenta (2019a).

### Geographic distribution

Guadeloupe.



**Fig. 16.** A–G. *Strobiligera cupella* sp. nov. A–B. Holotype, MNHN-IM-2000-38793, 15.8 mm. C. Paratype, MNHN-IM-2000-38794, 8.2 mm. D. Paratype, MNHN-IM-2000-38795, 8.3 mm. E–G. Paratypes, MNHN-IM-2000-38796, 11.5 mm, 10.8 mm. H–J. *Strobiligera* sp. B, MNHN, stn DW4550, 9.9 mm. Scale bars: A, C–F, H = 1 mm; B, G, I–J = 500  $\mu$ m.



**Bathymetric distribution**

320–428 m (empty shells), 300–370 m (live specimen).

*Strobiligera* sp. B

Fig. 16H–J

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4550; MNHN.

**Description**

Shell sinistral, conical, single complete shell up to 9.9 mm long and 2.0 mm wide, length/width ratio 4.8; apical angle of early whorls 17°. Protoconch paucispiral, 2.75 convex whorls, 0.85 mm long, 0.69 mm wide; first whorl dome-shaped, globose, mainly smooth but apparently with a few, minute pustules; subsequent whorls with two spiral cords, situated at 31% and 61% of whorl height, in addition to a much smaller subsutural cord; no axial sculpture. Teleoconch with up to 12 whorls; three main spiral cords, continuous with those of protoconch; adapical spiral cord very narrow and gradually enlarges through teleoconch, but never reaches same size as other cords; shallow suture, almost indistinct, with a smooth sutural cord; 19 slightly opisthocline axial ribs on 11<sup>th</sup> whorl; moderately large, rounded to slightly elliptical nodules; wide, smooth subperipheral cord, one smooth, very narrow basal cordlet, situated right below subperipheral one; no evident supranumerical cords; elliptical aperture, 1.18 mm long, 0.93 mm wide, length/width ratio 1.3; open, short anterior canal, 0.41 mm long, 0.42 mm wide, length/width ratio 1.0. Protoconch beige, teleoconch white.

**Remarks**

The protoconch size of *Strobiligera* sp. B falls within the range of *S. dinea* from Guadeloupe, and the adult shell of *Strobiligera* sp. B has a similar length (9.9 mm) to small adults of *S. dinea* (at least 11.1 mm). The beige protoconch of *Strobiligera* sp. B, apparently with minute pustules (but smooth and white in *S. dinea*), differentiates them. More material is needed to confirm these differences.

*Strobiligera* sp. B is also similar to *S. cupella* sp. nov., but the former has a small adult shell (reaching 9.9 mm in length vs up to 15.8 mm long in incomplete shells of *S. cupella*), the adapical spiral cord on the teleoconch is slightly more developed, and the protoconch is slightly elevated and larger (0.85 mm long, 0.69 mm wide vs 0.54–0.64 mm long, 0.49–0.52 mm wide in *S. cupella*).

**Geographic distribution**

Guadeloupe.

**Bathymetric distribution**

432–482 m (empty shell).

*Strobiligera* cf. *georgiana* (Dall, 1927)

Fig. 17A–B

*Triphora (Biforina) georgiana* Dall, 1927: 93.

*Triphora (Biforina) georgiana* – Abbott 1974: 112.

“*Triphora*” *georgiana* – Rolán & Fernández-Garcés 2008: 140, fig. 24a–e.

*Strobiligera georgiana* – Fernandes & Pimenta 2014: 169, fig. 1a.

**Type material**

**Lectotype**

USA • sh; off Georgia; depth 805 m; USNM 333516.

**Paralectotypes**

USA • 5 sh; same data as for lectotype; USNM 1592888.

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4550; MNHN.

**Emended description**

Shell sinistral, conical, up to 15.1 mm long (incomplete), 3.2 mm wide, apical angle of early whorls 20°. Protoconch multispiral, 3.75 whorls, 0.56 mm long, 0.44 mm wide; first whorl dome-shaped, with minute granules; subsequent whorls with two spiral cords, situated at 44% and 76% of whorl height; incomplete axial ribs (~27 ribs per whorl), with a smooth spiral zone above adapical spiral cord; abrupt transition to teleoconch. Teleoconch with 20 whorls (incomplete); two main spiral cords (median and abapical), with abapical one continuous with that of protoconch and median one emerging soon after; a very narrow adapical spiral cordlet more evident in late whorls, assuming a slightly nodulous appearance; shallow suture, almost indistinct, with a very narrow, smooth sutural cord; 14 slightly opisthocline axial ribs on 14<sup>th</sup> whorl; moderately large, nearly rounded to slightly elliptical nodules. Base not formed. Protoconch light brown, teleoconch beige (initial whorls whitish).

**Remarks**

The single shell from Guadeloupe is possibly not *S. georgiana* (illustrated in Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2014), but the incomplete base in both morphs precluded further comparisons. Differences comprise the color of the teleoconch (beige in the shell from Guadeloupe, white in the type material) and the orientation of axial ribs (slightly opisthocline in the shell from Guadeloupe, but nearly orthocline in the type material).

**Geographic distribution**

USA: Georgia (Dall 1927); Guadeloupe (this study).

**Bathymetric distribution**

Empty shells previously known from 805 m (Dall 1927). This study: 432–482 m (empty shell).

*Strobiligera* cf. *delicata* Fernandes & Pimenta, 2014

Fig. 17C–H

*Strobiligera delicata* Fernandes & Pimenta, 2014: 166, fig. 1b–k.

**Type material**

**Holotype**

BRAZIL • sh; off Espírito Santo State; 19°36' S, 38°53' W; depth 640 m; MNHN IM-2000-27528.

**Paratypes**

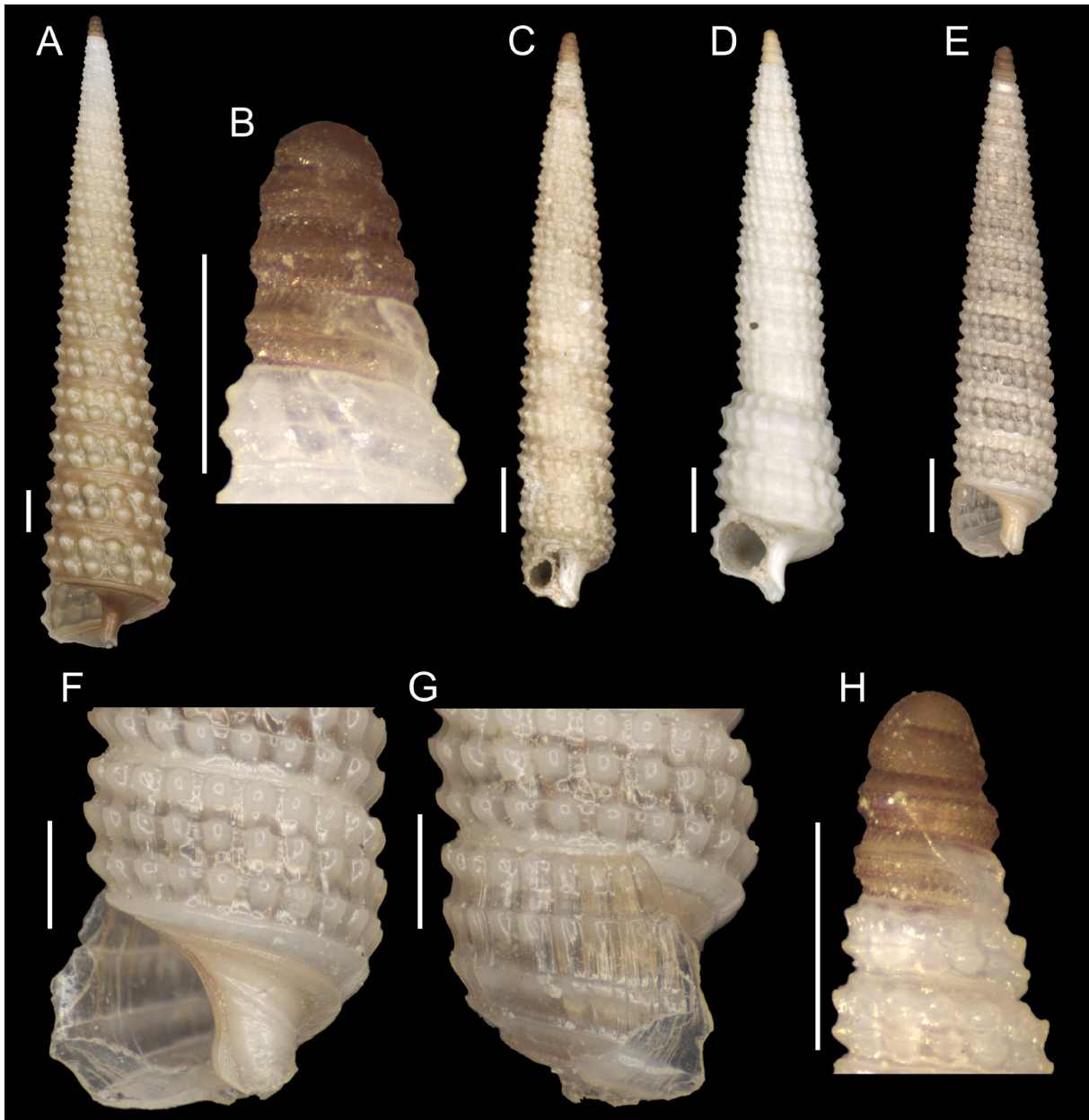
See Fernandes & Pimenta (2014).

**Material examined**

GUADELOUPE (Karubenthos 2 expedition) • 1 sh; stn DW4556; MNHN • 1 sh; stn DW4577; MNHN • 1 spec. stored dry; stn DW4635; MNHN.

**Emended description**

Shell sinistral, conical-fusiform, single complete shell up to 7.0 mm long (incomplete shells up to 8.9 mm long) and 1.5 mm wide, length/width ratio 4.7, apical angle of early whorls 18–20°; one shell with a distinct change in width on 13<sup>th</sup> teleoconch whorl, becoming broader. Protoconch multispiral, 3.5–4.0 whorls, 0.50–0.53 mm long, 0.34–0.37 mm wide; first whorl dome-shaped, with minute granules;



**Fig. 17.** A–B. *Strobiligera* cf. *georgiana* (Dall, 1927), MNHN, stn DW4550, 15.1 mm. C–H. *Strobiligera* cf. *delicata* Fernandes & Pimenta, 2014. C. MNHN, stn DW4556, 8.9 mm. D. MNHN, stn DW4577, 8.9 mm. E–H. MNHN, stn DW4635, 7.0 mm. Scale bars: A, C–E = 1 mm; B, F–H = 500  $\mu$ m.

subsequent whorls with two spiral cords, situated at 35% and 68% of whorl height; incomplete axial ribs (~33 ribs per whorl), with a smooth spiral zone above adapical spiral cord; abrupt transition to teleoconch. Teleoconch with up to 17 whorls (incomplete); three main spiral cords, with median and abapical cords continuous with those of protoconch; adapical spiral cord initially narrow, but gradually enlarging and reaching nearly same size as other cords between 11<sup>th</sup> and 13<sup>th</sup> whorls; shallow suture, almost indistinct, with a very narrow, smooth sutural cord; 18–19 orthocone axial ribs on 14<sup>th</sup> whorl; medium-sized to moderately large, nearly rounded to slightly elliptical nodules; wide, smooth subperipheral cord, two smooth basal cords, adapical one prominent and close to subperipheral one, abapical cord narrow and more distant; no evident supranumerical cords; elliptical aperture, 1.0 mm long, 0.69 mm wide, length/width ratio 1.5; open, very short anterior canal, 0.14 mm long, 0.20 mm wide, length/width ratio 0.7. Protoconch light brown, teleoconch white to dirty-white.

### Remarks

Shells of *S. cf. delicata* from Guadeloupe are very similar to the type material from SE Brazil, and their planktotrophic development could allow such a wide geographic range. The single adult shell from Guadeloupe is 7.0 mm long and incomplete shells reach up to 8.9 mm, contrasting with adult shells from Brazil, reaching only 5.8 mm. This difference in length might be related to the later development of the adapical spiral cord on the teleoconch in shells from Guadeloupe, reaching nearly the same size as other cords between the 11<sup>th</sup>–13<sup>th</sup> whorls vs the eighth–tenth whorl in the type material. More adult shells from Guadeloupe are required in order to evaluate the importance of these differences.

The most similar species to *S. cf. delicata* in Guadeloupe is *S. cf. georgiana*, which has a much reduced adapical spiral cord, fewer axial ribs on the teleoconch, a slightly opisthocline orientation of the axial ribs (vs orthocone in *S. cf. delicata*) and a larger and more conical shell. These differences were already pointed out by Fernandes & Pimenta (2014) when they compared the types of both species.

One atypical shell of *S. cf. delicata* has a distinct change in width on the 13<sup>th</sup> teleoconch whorl, becoming broader (Fig. 17D). This is also observed in *S. torticula* (Rolán & Fernández-Garcés 2008; Fernandes & Pimenta 2015b), which in contrast is much larger (incomplete shell reaching up to 25.0 mm in length – Rolán & Fernández-Garcés 2008) than *S. cf. delicata*. In addition, the protoconch of *S. torticula* has almost five whorls and it is 0.64 mm long and 0.45 mm wide (Fernandes & Pimenta 2015b) vs 3.5–4.0 whorls, 0.50–0.53 mm long and 0.34–0.37 mm wide in *S. cf. delicata*.

### Geographic distribution

Guadeloupe (this study); Brazil: off Espírito Santo and Rio de Janeiro (Fernandes & Pimenta 2014).

### Bathymetric distribution

Empty shells previously known from 607–940 m (Fernandes & Pimenta 2014). This study: 358–428 m (empty shells), 265–268 m (live specimen).

### *Strobiliger* cf. *ibex* (Dall, 1881)

Figs 18–20

*Triforis ibex* Dall, 1881: 86.

*Triforis* (*Sychar*) *inflata* var. *ibex* – Dall 1889a: 249, pl. 20 fig. 12b; 1889b: 138, pl. 20 fig. 12b.

*Triphora* (*Strobiliger*) *inflata* var. *ibex* – Dall 1924: 89. — Abbott 1974: 112, fig. 1148a (a reproduction of Dall's illustration).

*Inella ibex* – Rolán & Fernández-Garcés 2008: 110, figs 14k–m, 36g (the latter a reproduction of Dall's illustration).

*Strobiligera ibex* – Fernandes & Pimenta 2014: 169; 2019a: fig. 2o–p.

non *Inella colon* Dall, 1881 – Rolán & Fernández-Garcés 2008: fig. 16e–f.

### Type material

#### Lectotype

CUBA • sh; Yucatán Strait, off Cape San Antonio; depth 1170 m; MCZ 7391.

Rolán & Fernández-Garcés (2008) argued that “three localities [off Cuba, Yucatan Strait and Cape San Antonio] mentioned in the original description are written on the label of the lectotype, and hence there is no exact information about which locality applies to this type”. These localities mainly refer to the same part of the ocean, i.e., the narrowest distance between Cuba and Mexico, and Dall (1881) provided the same depth (640 fms = 1170 m) for Yucatán Strait and off Cape San Antonio. Following the MCZ catalogue book for the lectotype, the type locality is as listed above.

#### Paralectotypes

CUBA • 1 sh; same data as for lectotype; USNM 87313 • 1 sh; off Havana; depth 823 m; MCZ 7392.

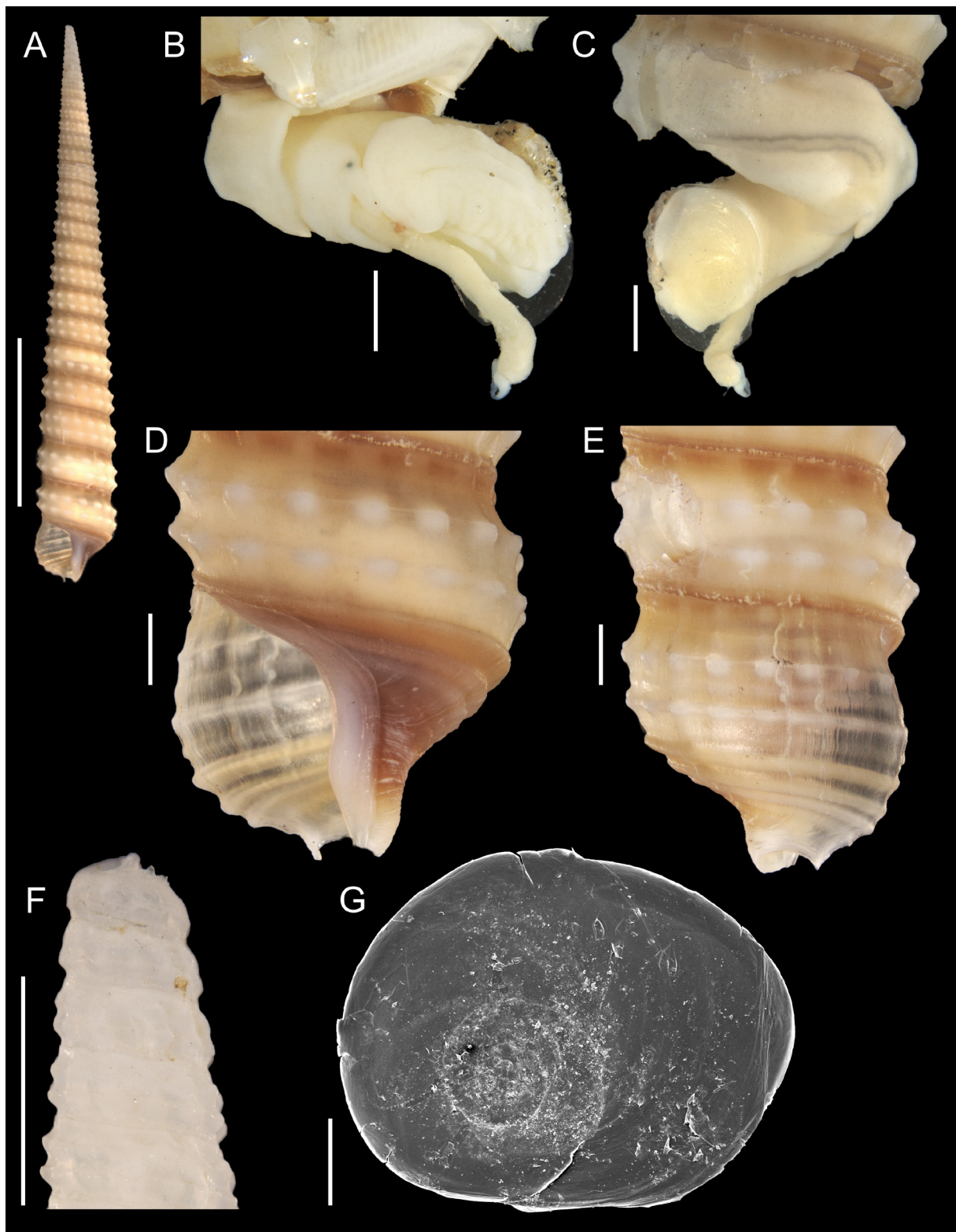
### Material examined

GUADELOUPE (Karubenthos 2 expedition) • 1 spec. stored in ethanol; stn CP4618; MNHN-IM-2013-61225.

### Emended description

Shell sinistral, conical-fusiform, much elongated, up to 33.3 mm long, 5.0 mm wide, length/width ratio 6.7, apical angle of early whorls 14°. Protoconch broken. Teleoconch with at least 28 whorls; two main spiral cords (median and abapical), with a very narrow adapical spiral cordlet becoming more evident in late whorls, remaining weak on body whorl but slightly nodulous; distinct suture, with a narrow, smooth sutural cord; 15 slightly opisthocline axial ribs on 24<sup>th</sup> whorl (regarding broken apex); medium-sized, slightly elliptical nodules; wide, smooth subperipheral cord, two smooth basal cords right below it; three supranumerical cords, below each spiral cord (supranumerical cord below abapical spiral cord weakest); elliptical aperture, 3.4 mm long, 2.2 mm wide, length/width ratio 1.5; open, very short anterior canal, 0.45 mm long, 0.80 mm wide, length/width ratio 0.6. Shell mainly beige, with suture, adapical spiral cordlet and base light brown, and eight initial teleoconch whorls whitish.

Head-foot white, with part of intestine greyish; very reduced eyes; extended proboscis reaches 3.3 mm in length, 4.8× as long as extended cephalic tentacles (0.69 mm long); pedal slit covering 71% of foot length. Operculum elliptical, flat, semi-transparent, with poorly distinct whorls, nucleus slightly eccentric, dislocated 31% from center toward margin; diameter of opercular pouch 83% of diameter of operculum. Inner side of jaw with scales gem-shaped (typically 20.6–24.0 µm long, 7.6–8.4 µm wide, ratio length/width 2.7–2.8) at margins, or leaf-shaped (typically 31.8–34.9 µm long, 14.0–15.8 µm wide, ratio length/width 2.0–2.5) at middle portion; outer side of jaw with scales mainly rectangular (16.9–51.1 mm long, 5.1–21.9 mm wide, ratio length/width 2.3–3.7), rectangular-bilobed (23.8–26.9 µm long, 10.0–11.2 µm wide, ratio length/width 2.1–2.5), squared (13.4–22.6 µm long), hexagonal (14.5–17.4 µm long, 13.0–14.1 µm wide, ratio length/width 1.1–1.2) or curved with extremities slightly to considerably unequal in width (21.0–25.4 µm long, 9.8–14.2 µm wide, ratio length/width 1.6–2.6). Radula with little differentiation in teeth morphology, formula not discernible (but at least 27 overcrowded teeth per row); all teeth with elongated cusps and a small basal area; central tooth scissor-like, with two equal cusps, 2.4–2.8 µm wide; remaining teeth 2.5–3.6 µm wide, with three cusps, innermost (cusp 1) often thinner and shorter (~50–75% of length) than cusps 2 and 3, but occasionally reaching same length.

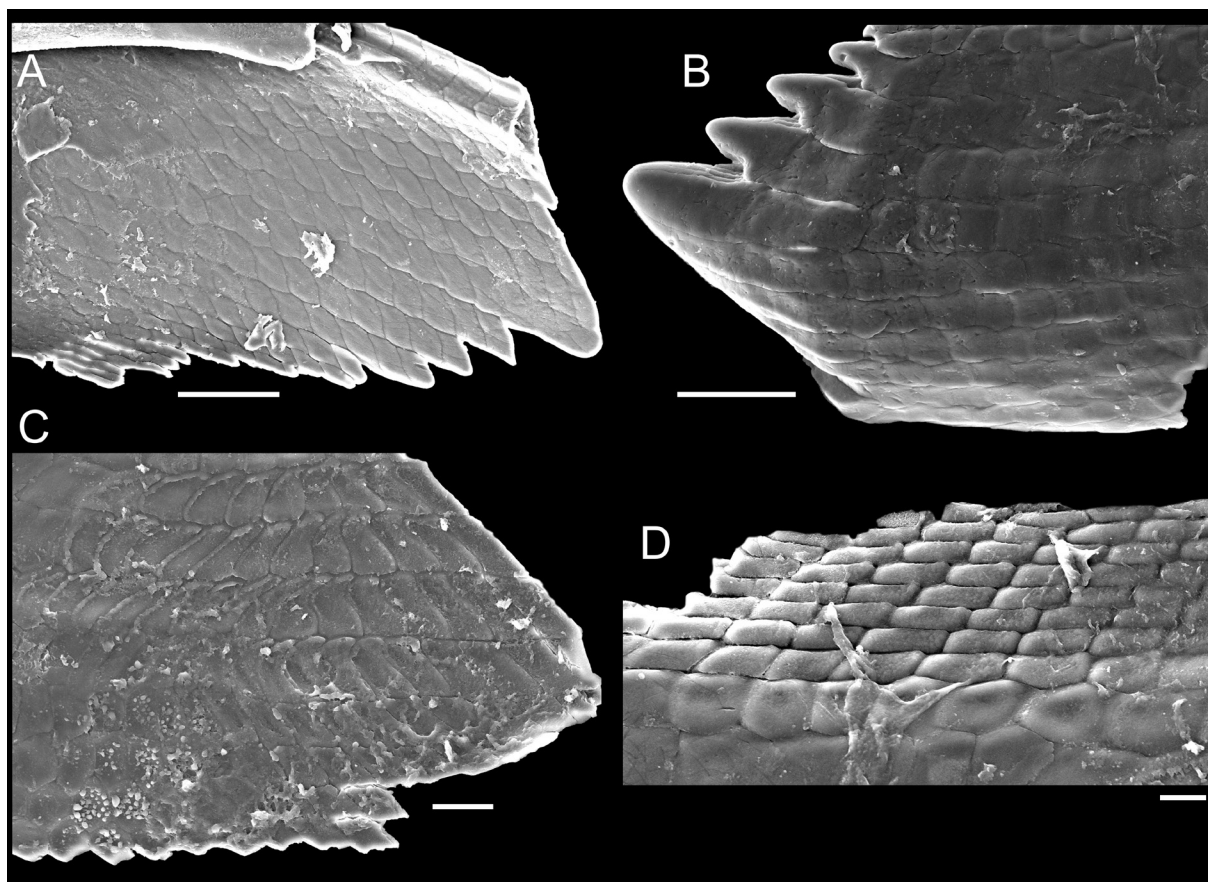


**Fig. 18.** *Strobiligera* cf. *ibex* (Dall, 1881), MNHN-IM-2013-61225, stn CP4618, 33.3 mm. Scale bars: A = 1 cm; B–F = 1 mm; G = 500  $\mu$ m.

### Remarks

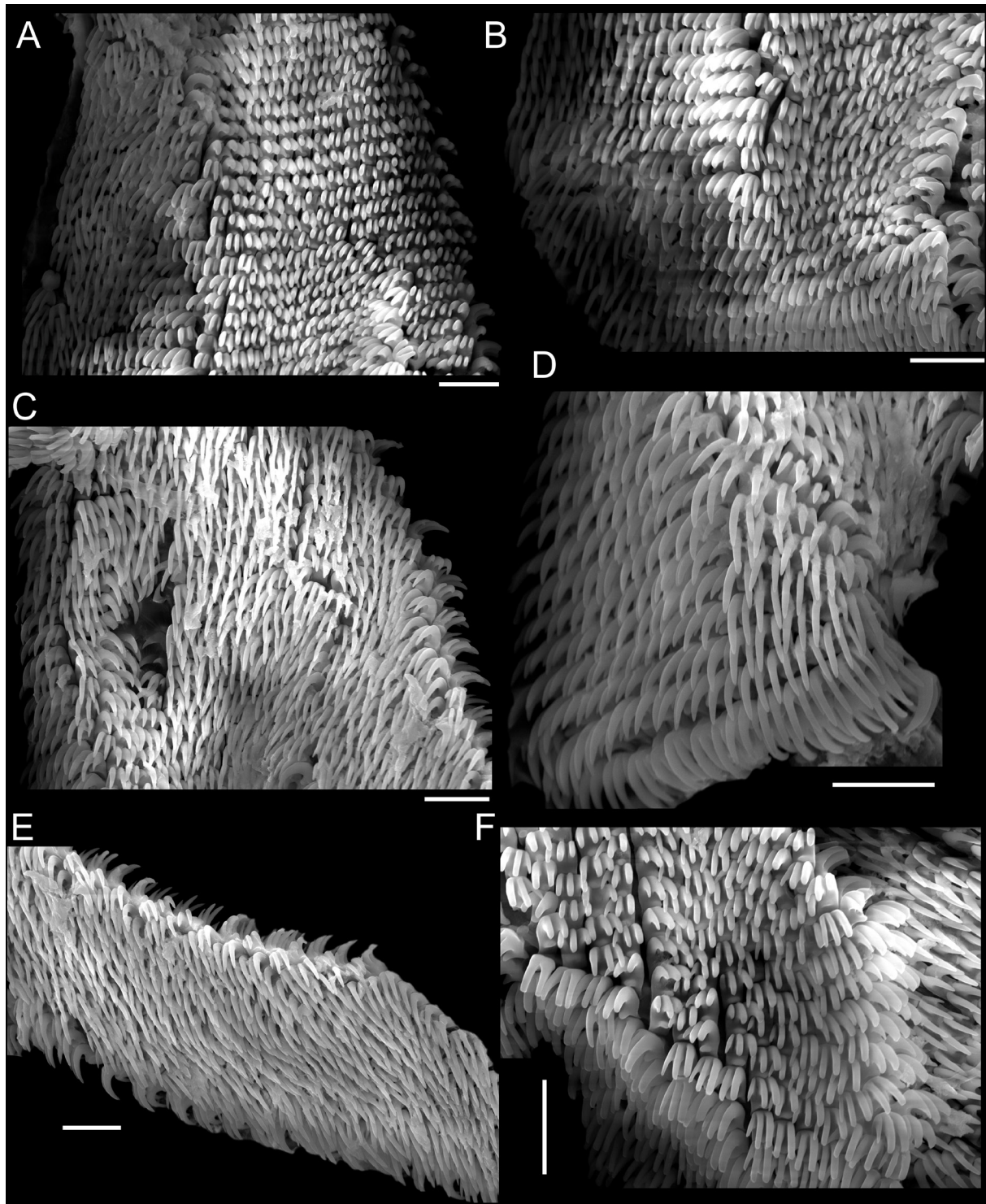
The single specimen from Guadeloupe is an extremely large adult (33.3 mm long for at least 28 teleoconch whorls – apex broken), 3× as long as the maximum length of the type material of up to only 11.0 mm (Dall 1881). Based on Dall (1881) and the subsequent drawing by Dall (1889a), *S. ibex* has 19 teleoconch whorls (apex broken), contrasting with the shell designated as lectotype by Rolán & Fernández-Garcés (2008), which is 10.4 mm long for ~14 teleoconch whorls (apex broken) and apparently has a more distinct last whorl than the shell illustrated by Dall (1889a). It is possible that there is more type material of *S. ibex* hidden in some collections that has not been imaged yet; e.g., Dall (1881) described a complete protoconch, which has not been reported again in the recent literature. Apart from the difference in shell size, the original description, the drawing and available photographs of the types are in considerable agreement with the specimen from Guadeloupe, including the excavated suture and very late development of the adapical spiral cord on the teleoconch [whereas the similar *Strobiligera colon* (Dall, 1881) comb. nov. has an indistinct suture and adapical cord], the presence of two basal cords in addition to the subperipheral cord (Dall 1881) and the reduced anterior canal (disproportional in relation to the shell length).

The specimen from Guadeloupe is nearly identical to two shells from Mexico and the Straits of Florida identified as *I. colon* by Rolán & Fernández-Garcés (2008: fig. 16e–f), but these authors recognized the possibility of an erroneous identification. These two shells reach 20.3 mm and 29.4 mm in length, with broken apex. Fernandes & Pimenta (2019a) recognized the similarity between these two shells and the



**Fig. 19.** *Strobiligera* cf. *ibex* (Dall, 1881), MNHN-IM-2013-61225, stn CP4618. A. Inner jaw. B–D. Outer jaw. Scale bars: A–B = 50  $\mu$ m; C = 20  $\mu$ m; D = 10  $\mu$ m.

holotype (but not all shells) of *S. unicornium*, described from NE Brazil (Simone 2006). In fact, the description of the protoconch of *S. ibex* by Dall (1881) is very similar to the protoconchs tentatively assigned to *S. unicornium* by Fernandes & Pimenta (2019a). The holotype of *S. unicornium* has a broken



**Fig. 20.** *Strobiligera* cf. *ibex* (Dall, 1881), MNHN-IM-2013-61225, stn CP4618, radula; the central tooth, bearing two cusps, is shown in the left side of fig. F. Scale bars: 10  $\mu$ m.



apex, and the broad interpretation of *S. unicornium* by Fernandes & Pimenta (2019a) encompasses shells with a highly varied development of the adapical spiral cord on the teleoconch, although more or less in a continuum. More material (with protoconch) from these deep-sea triphorids is necessary prior to suggesting any synonymy.

The eyes of *S. cf. ibex* (Fig. 18B) are more reduced than those of “*I.*” *longissima* (Fig. 2C), suggesting that *S. cf. ibex* is restricted to the continental slope.

### Geographic distribution

USA: Straits of Florida (Dall 1889b; Rolán & Fernández-Garcés 2008 – determined as *I. colon*); Mexico (Rolán & Fernández-Garcés 2008 – determined as *I. colon*); off Cuba (Dall 1881); Guadeloupe (this study).

### Bathymetric distribution

Empty shells previously known from 236–1170 m (Dall 1881; Rolán & Fernández-Garcés 2008 – determined as *I. colon*). This study: 780–828 m (live specimen).

### *A digression: description of a new species of Strobiligera from Brazil*

*Strobiligera carioca* sp. nov.

[urn:lsid:zoobank.org:act:3D4D214A-711A-4BB0-B16B-53C60CF95B68](https://doi.org/10.3897/zoobank.org/act:3D4D214A-711A-4BB0-B16B-53C60CF95B68)

Fig. 21

non *Triphora compsa* Dall, 1927 – Absalão 1989: 3.

non *Inella apexbilitata* Rolán & Fernández-Garcés, 2008 – Fernandes & Pimenta 2019a: 9, fig. 4.

### Diagnosis

Light brown/beige shell; protoconch with a small nucleus; adapical spiral cord of teleoconch reaching same size as other spiral cords between eighth and twelfth whorl.

### Etymology

The specific epithet alludes to the citizens of Rio de Janeiro, referring to the restricted geographic range of the species to this state. Epithet as a noun in apposition.

### Type material

#### Holotype

BRAZIL • sh; Rio de Janeiro State, Campos Basin; 22°48' S, 40°45' W; depth 106–110 m; 27 Jan. 1998; MNRJ 36601.

#### Paratypes

BRAZIL • 3 sh; same data as for holotype; IBUFRJ 23518.

### Additional material examined

See Fernandes & Pimenta (2019a) for the species previously determined as *I. apexbilitata*. The holotype and paratypes were removed from IBUFRJ 19577, which remains as ordinary material.

### Description

See Fernandes & Pimenta (2019a) for the species previously determined as *I. apexbilitata*.

## Remarks

As addressed by Fernandes & Pimenta (2019a), most adult shells of this species are larger than shells of *I. apexbilarata*, described from the Bahamas, although there are small adults of *S. carioca* sp. nov., reaching 4.2 mm in length (Fernandes & Pimenta 2019a: fig. 4e) vs 3.5 mm in *I. apexbilarata*. The authors argued that their main differences are related to shell color and bathymetric range (*S. carioca*: mid-end of continental shelf; *I. apexbilarata*: bathyal). In addition, the abapical spiral cord is slightly more developed in the Bahamian species (Rolán & Fernández-Garcés 2008), whereas the median cord is more developed than other cords on the initial whorls of the teleoconch in *S. carioca*. The adapical spiral cord of the teleoconch reaches nearly the same size as other cords between the eighth and twelfth whorls in *S. carioca*, but it is much less developed until the eighth whorl in *I. apexbilarata*. Considering all these differences and their non-planktotrophic development, these species probably have restricted geographic ranges, and neither of them was sampled from Guadeloupe by the Karubenthos 2 expedition.

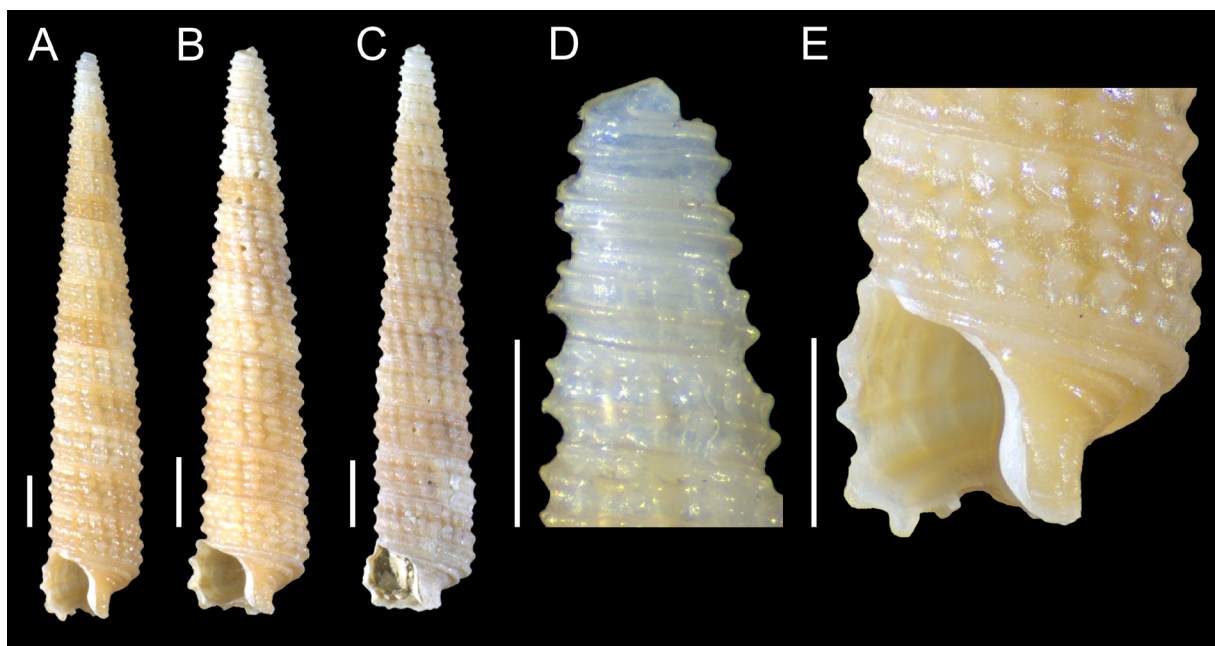
All material of *S. carioca* sp. nov. listed by Fernandes & Pimenta (2019a – as *I. apexbilarata*) and stored in IBUFRJ is available, whereas that from MNRJ and MORG (Museu Oceanográfico “Prof. Eliézer de Carvalho Rios”, Rio Grande, Brazil) was lost during the 2018 fire in MNRJ. The single shell listed from Espírito Santo State (IBUFRJ 19619) was indicated as a very worn juvenile and therefore this record needed confirmation (Fernandes & Pimenta 2019a). Yet, after a new evaluation, this shell cannot be confidently assigned to this species. Thus, this species is currently known only from Rio de Janeiro State.

## Geographic distribution

Brazil: Rio de Janeiro State.

## Bathymetric distribution

Empty shells from 69 to 163 m (Fernandes & Pimenta 2019a).



**Fig. 21.** *Strobiligera carioca* sp. nov. **A, D–E.** Holotype, MNRJ 36601, 11.1 mm. **B–C.** Paratypes, IBUFRJ 23518, 8.1 mm, 8.6 mm. Scale bars: A–C, E = 1 mm; D = 500  $\mu$ m.

## Discussion

### The findings of the Karubenthos 2 expedition

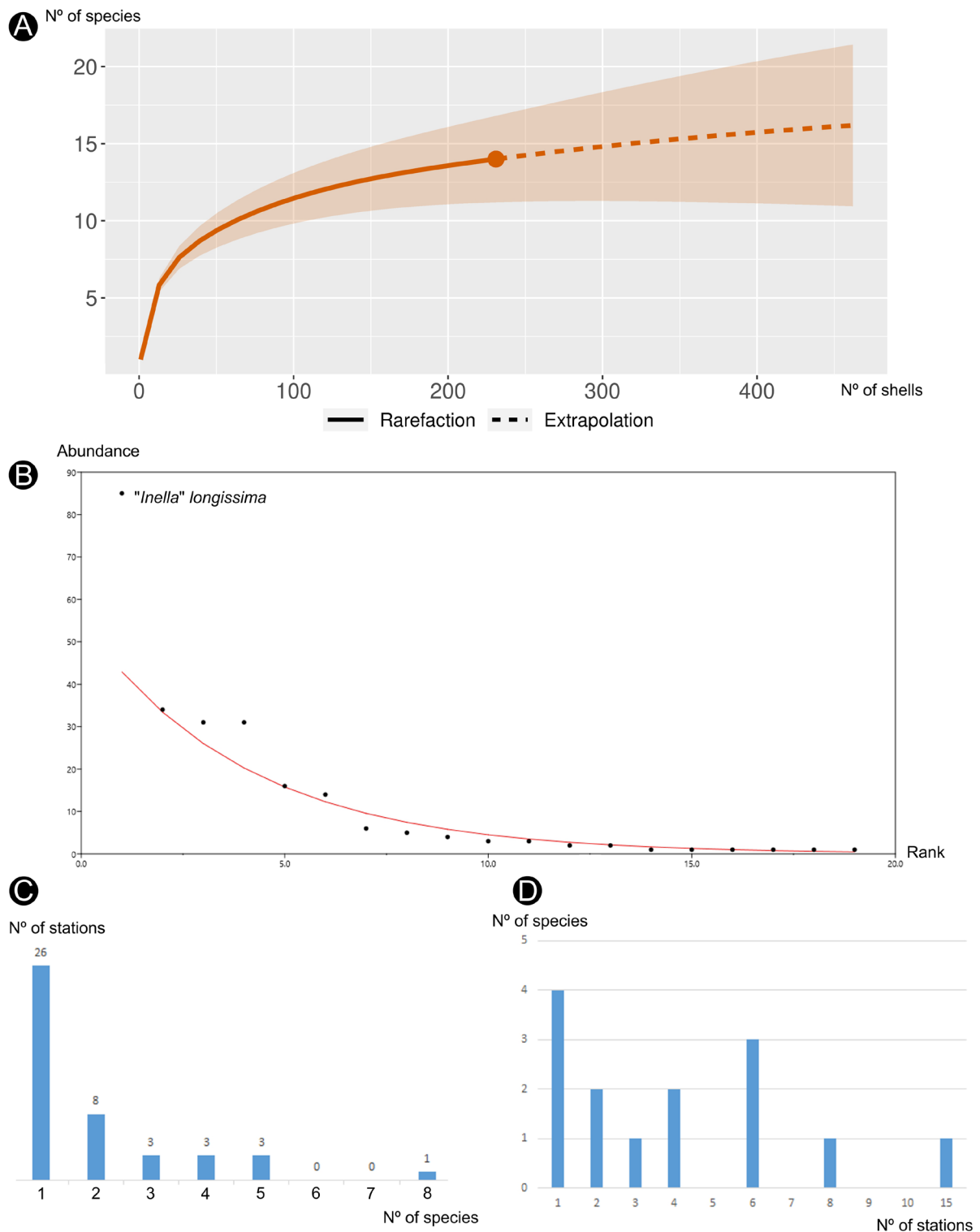
In comparison with the 29 and 33 triphorid species found in the shallow waters from respectively Guadeloupe (Rolán & Fernández-Garcés 2015; Fernandes 2024) and Martinique (Fernandes 2024), the Karubenthos 2 expedition yielded 14 deep-sea triphorid species (i.e., species typically found below 200 m) from Guadeloupe. The coverage-based rarefaction and extrapolation of triphorids from the Karubenthos 2 expedition is fairly saturated (Fig. 22A), and the estimation of sample coverage (SC) is 98.7%. So, with the addition of “*I.*” aff. *harryleei* by Lamy & Pointier (2018), there are currently 15 deep-sea triphorids from Guadeloupe. This is a surprisingly high number for a deep-sea habitat, as the diversity of Triphoridae is assumed to be much greater in shallow waters (Marshall 1983). Of all 159 stations from Karubenthos 2 (including those shallower than 100 m, and stations which contained worn, unidentified triphorids), 48 (30.2%) contained triphorids, of which four were sampled by benthic beam trawls (13.8% of the 29 stations) and 44 by a Warén dredge (33.8% of the 130 stations).

The abundance distribution showed that “*I.*” *longissima* was by far the most common species from the deep waters of Guadeloupe (Fig. 22B). Restricting to stations below 100 m deep, most stations had one or two triphorid species, but some up to eight species (Fig. 22C), and only “*I.*” *longissima* was sampled at more than 10 stations, i.e., 15 (Fig. 22D). Stations which had at least three triphorid species (herein regarded as ‘hyper-diverse stations’) were found in three main groups around the archipelago: between Marie-Galante and Îles des Saintes; east of La Désirade; and north of Île de Basse-Terre (Fig. 23). These hyper-diverse stations comprised both narrow depth ranges (e.g., DW4572 and DW4635, 3 m of depth range; DW4599 and DW4646, 4 m of depth range) to very broad depth ranges (e.g., DW4555, 158 m of depth range).

### The need for live specimens in order to refine taxonomic identifications

The absence of color in most deep-sea triphorid shells means one feature less that is commonly used to separate shallow-water triphorid species. To complicate even further the taxonomy of deep-sea triphorids, most species have a paucispiral protoconch (indicative of non-planktotrophic development), which provides fewer taxonomic data than a multispiral protoconch (usually indicative of planktotrophic development). Moreover, paucispiral protoconchs are prone to convergence in unrelated lineages (Fernandes & Pimenta 2019a, 2020). Thus, the identification of deep-sea triphorids requires careful examination in order not to overlook important differences between species (Dall 1881: 85). Most West Atlantic deep-sea triphorids were described by Dall (1881, 1889a, 1927), but unfortunately several of these species are only known from worn shells, often without the protoconch. Further studies, including new material from Cuba and SE USA (from where Dall described most deep-sea triphorids), are necessary to validate these species. It is also necessary to revise Dall’s type material to match with the respective descriptions, in order to solve problems that relate to earlier lectotype designations (Fernandes & Pimenta 2019a; Gofas *et al.* 2023; this study). The present study attempts to maximally use Dall’s names instead of creating new names when only subtle differences were observed between the material from Guadeloupe and that studied by Dall. Yet, this strategy may turn out to be erroneous because the records from Guadeloupe are sometimes thousands of kilometers away from the type localities, which could imply a geographic isolation for these mostly non-planktotrophic species (i.e., possibly with restricted ranges). However, without knowing the morphological variation in the species described by Dall and considering the lack of studies on deep-sea triphorids in sites between Guadeloupe and Cuba or SE USA, it seems for the time being wise to opt for a conservative approach by keeping Dall’s names as much as possible. Ideally, the study of soft parts and DNA would help to clarify this taxonomic puzzle.

As cited in the Results section, Lamy & Pointier (2018) already recorded “*I.*” *longissima* and *S. variabilis* sp. nov. (under the name *Triphora* sp. 2) from the deep waters of Guadeloupe, whereas their record of

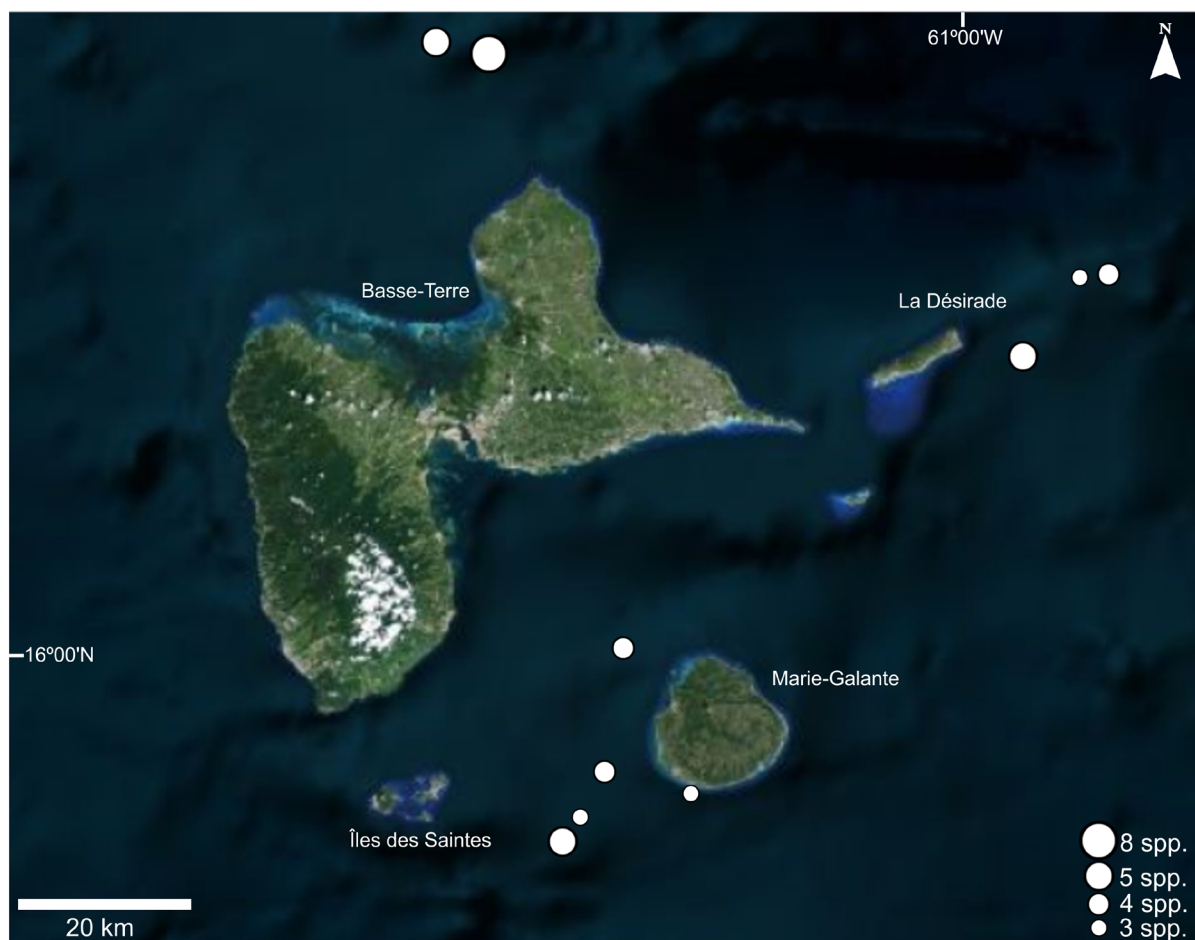


**Fig. 22.** A. Coverage-based rarefaction and extrapolation of triphorids from the Karubenthos 2 expedition; the shadowed area indicates the 95% confidence interval. B. Abundance distribution of triphorids from Karubenthos 2. C. Number of triphorid species sampled per number of stations. D. Number of Karubenthos 2 stations at which each triphorid species was sampled.

“*I.*” aff. *harryleei* (with unknown protoconch) was not recovered in the present study. Other deep-sea records from Guadeloupe by Lamy & Pointier (2018) are: *Triphora* sp. 1 (200 m deep), which corresponds to a cerithiopsid genus, probably *Belonimorphis* Jay & Drivas, 2002; *Triphora* sp. 3 (300 m deep), which corresponds to a worn shell of *Iniforis* sp., without apex, probably dislodged from shallow waters; and *Triphora* sp. 4 (300 m deep), which corresponds to a juvenile shell of uncertain identification, but resembling “*Inella*” *faceta* Fernandes & Pimenta, 2019, currently known only from Brazil, at depths between 32 and 160 m.

#### Another discussion about *Inella* and related genera

The taxonomic debate about the distinction between *Inella* Bayle, 1879, with its type species from shallow waters of the Indo-Pacific [*Inella gigas* (Hinds, 1843), with unknown protoconch from the type material] and *Strobiliger* Dall, 1924, with its type species from deep waters of the West Atlantic [*Strobiliger ibex* (Dall, 1881), also with unknown protoconch from the type material], remains after decades (Fernandes & Pimenta 2019a). Briefly, Marshall (1983: 19) observed some radular differences between one species of each genus, but the very limited knowledge about the radulae of both genera precluded further decisions. Bouchet (1985: 29) speculated that *Strobiliger* could be a synonym of *Inella*, but he preferred “to use *Strobiliger*, of which there is no doubt that it constitutes a uniform group, restricted to the Atlantic circumlittoral deep and the bathyal” [translated from French]. Rolán &



**Fig. 23.** Hyper-diverse stations of Triphoridae Gray, 1847 from the Karubenthos 2 expedition, containing at least three species. Map obtained from Google Earth.

Fernández-Garcés (2008) treated *Strobiligera* as a synonym of *Inella*, but many species allocated by them to *Inella* are currently assigned to the informal group “pseudo *Inella*” (Fernandes & Pimenta 2019a) and require new generic allocations. Fernandes & Pimenta (2014, 2019a) suggested that the type species of *Strobiligera* and several other West Atlantic species with paucispiral protoconchs have a much more inflated first protoconch whorl than typical species of *Inella*, and that these genera might be phylogenetically close. However, the interpretation by Fernandes & Pimenta (2014, 2019a) regarding the paucispiral protoconch of *Inella* was based on Marshall (1983) and might turn out to be erroneous after the analysis of additional material from the type locality of *I. gigas*.

After the study of the material from Guadeloupe, some species (e.g., Figs 7–8) appear to be an intermediate stage between the inflated (Figs 13–16) and narrow (Figs 9–12) first protoconch whorl. In addition, the ongoing molecular phylogeny of Triphoroidea (in prep.) indicates a monophyletic condition for a group (currently with very few DNA sequences) comprising West Atlantic species with inflated or narrow first protoconch whorl, although more DNA sequences are required, especially for Indo-Pacific species. Following Bouchet’s (1985) view, it is possible that all Atlantic deep-sea species form a single unit, but it is also possible that *Inella* is a cosmopolitan genus with a broad bathymetric range and shell morphology. Albeit Marshall (1983: 19) cited the existence of species of *Inella* from the Indo-Pacific with planktotrophic development, which would enable a comparison with the planktotrophic species currently allocated under *Strobiligera*, those species still need to be better imaged (Fernandes & Pimenta 2019a). Based on the species of *Inella* currently listed on MolluscaBase (2023), I searched for Indo-Pacific species with a multispiral protoconch derived from a planktotrophic development. Some generic allocations are evidently incorrect, and they are listed below in order to facilitate further comparisons:

- (1) *Inella pagoda* (Hinds, 1843) and *Inella vittata* (Hinds, 1843) actually belong to *Viriola* Jousseaume, 1884, as previously indicated in the literature (see synonymic lists of both species in Bakker & Albano 2022).
- (2) *Inella sculpta* (Hinds, 1843) was illustrated by Albano *et al.* (2019). Its teleoconch morphology is totally different from that of *I. gigas*, and a more adequate generic allocation is *Euthymella sculpta* (Hinds, 1843) comb. nov.
- (3) *Inella blainvilli* Jousseaume, 1884, *Inella perimensis* Jousseaume, 1898 and *Inella rossiteri* Jousseaume, 1884 were recently illustrated by Albano *et al.* (2023). They have a late median spiral cord on the teleoconch, contrasting with the initially weak adapical cord in *Inella*. Their multispiral protoconch with one spiral cord suggests they belong to *Bouchettriphora* Marshall, 1983 or *Obesula* Jousseaume, 1898, despite the apparent reticulated first protoconch whorl in *I. perimensis* (Albano *et al.* 2023: fig. 61o); analysis of soft parts is required in order to properly allocate these species.
- (4) *Inella numerosa* Jousseaume, 1898 was illustrated by Albano *et al.* (2023). The lectotype has initially three spiral cords on the teleoconch and a multispiral protoconch with a reticulated first whorl and a larval shell with one spiral cord. Based on the considerations by Marshall (1983, 1994) about *Tetrastoma* Laseron, 1958 (which is a junior homonym of *Tetrastoma* Philippi, 1865 – Beu 2004) and the possibly related *Costatophora* Marshall, 1994, this species is here referred to as *Costatophora numerosa* (Jousseaume, 1898) comb. nov. The species currently grouped in *Costatophora* (MolluscaBase 2023) may belong to unrelated lineages given the discrepant teleoconch morphology of the type species, with a weak spiral sculpture in late whorls (Marshall 1994). Yet, the present generic allocation of *C. numerosa* (with three nearly equal spiral cords on the first teleoconch whorl, just like the type species of *Costatophora*, in addition to a similar protoconch morphology) is justified due to the previous inadequate allocation under *Inella* (whose type species has a weak adapical spiral cord on the teleoconch).

Most of the remaining Indo-Pacific species of *Inella* listed in MolluscaBase (2023) have unknown protoconchs or they are poorly illustrated in the literature or they are paucispiral. Based on the drawing

by Laseron (1958) of *Inella acicula* Laseron, 1958 and the photograph by Mulochau *et al.* (2020) of *Inella asperrima* (Hinds, 1843), their many-whorled protoconchs seem identical to that of *Subulophora* Laseron, 1958, despite lacking a better illustration of the protoconch sculpture in those works. In fact, Marshall (1983) already considered *Inella* and *Subulophora* as closely related genera, e.g., by sharing an initially weak adapical spiral cord on the teleoconch, despite some radular differences (but see below); agreeing with him, *Subulophora* and *Hypotriphora* Cotton & Godfrey, 1931 are probably synonyms, pending knowledge about the radula of the latter. The fossil species *Subulophora fritschi* (Koenen, 1883), from the Miocene (and perhaps also part of the Oligocene and Pliocene – Bakker & Albano 2022) of Europe, has a multispiral protoconch typical of the genus (Marquet 1996), and it is the single European species currently allocated in *Subulophora* (but already allocated in *Inella* – Lozouet *et al.* 2001), a genus mostly composed of Recent Indo-Pacific species (MolluscaBase 2023). The type species of the fossil genus *Norephora* Gründel, 1975, i.e., *Norephora granulata* (Strauch, 1967) from the Oligocene of Europe, was already suggested to probably belong to *Subulophora* (Fernandes & Pimenta 2014). Accordingly, several other European fossil species currently allocated to *Norephora* in MolluscaBase (2023) have a multispiral protoconch like *Subulophora*, from the Early Paleocene (Amitrov & Zhegallo 2007: pl. 3 fig. 5) to the Late Oligocene [Schnetler *et al.* (2024), for *Norephora elatior* (Koenen, 1891)]. One Danian fossil from the Early Paleocene, determined as *Epetrium separabilis* (Ravn, 1933) by Lauridsen & Schnetler (2014), could also be argued as an ancient form linked to *Norephora* or *Subulophora*. Younger European fossils with a similar teleoconch morphology, from the Miocene to the Pliocene, mainly have a paucispiral protoconch (with the exception of *S. fritschi*), indicative of non-planktotrophic development (Marquet 1996; Lozouet 1999; Landau *et al.* 2018), perhaps somehow related to environmental modifications with the gradual closure of the Tethys Sea. Landau *et al.* (2018) synonymized *Norephora* with *Inella*, and I consider that possibly *Norephora*, *Subulophora* and *Hypotriphora* might be further confirmed as synonyms of *Inella* (see below), pending more data about the type species *I. gigas*. There are no Indo-Pacific fossil species of *Subulophora* listed in MolluscaBase (2023), and the oldest known Indo-Pacific fossil species of *Inella* is from the Eocene of New Zealand [Bakker & Albano (2022), for *Inella aoteaensis* (Marshall & Murdoch, 1920), with unknown protoconch] or the Late Eocene of West Australia (*Inella dauciformis* Darragh, 2017, with a paucispiral protoconch, and *Inella moniliferata* Darragh, 2017, with unknown protoconch). Thus, it is possible that *Inella* s. lat. (combined with *Norephora* and *Subulophora*) originated in the Early Paleocene of Europe and further spread via the Tethys Sea to what is currently known as the Indo-Pacific.

The dome-shaped protoconch of species of *Strobiligera* with planktotrophic development contrasts with the acuminate (and often many-whorled) protoconch of *Norephora* and *Subulophora* (Fernandes & Pimenta 2014). To my knowledge, the oldest record of a species of *Strobiligera* is that of *Strobiligera cristulata* (Sacco, 1895), from the Pliocene of the Mediterranean (Landau *et al.* 2006). A genetic divergence between three West Atlantic species of *Strobiligera* and one Indo-Pacific sequence from GenBank determined as *Subulophora peasi* (Jousseume, 1884) is also observed in the ongoing molecular phylogeny (in prep.), but requiring more DNA sequences. For the moment, probably the most valuable argument for the validation of *Strobiligera* comes from the radula: the single radula so far known of *Inella* from the Indo-Pacific (Marshall 1983), i.e., of *Inella obliqua* (May, 1915), has differentiated central (five cusps), lateral (four cusps) and marginal (three cusps) teeth; the central and lateral teeth of *I. obliqua* are very similar to the single known radula of *Subulophora*, i.e., from the type species *Subulophora rutilans* (Hervier, 1897), also illustrated by Marshall (1983). The radula here studied for *Strobiligera* cf. *ibex* (Fig. 20) is the fourth on this Atlantic genus (Bouchet 1985; Bouchet & Warén 1993; Fernandes & Pimenta 2019b). The teeth of *Strobiligera* usually bear two to three prominent cusps depending on the species, and the radula is nearly undifferentiated in each species, at least at first sight. In the East Atlantic species *Strobiligera brychia* (Bouchet & Guillemot, 1978), the outer marginal teeth are smaller and apparently without the minute structures besides the two cusps (Bouchet 1985). In the East Atlantic species *Strobiligera lubrica* Bouchet & Warén, 1993, the outer marginal teeth were

described with three cusps vs two cusps in the remaining teeth, in addition to a clear size reduction of the outer marginal teeth (Bouchet & Warén 1993: fig. 1285). This size reduction of outer marginal teeth is also observed in the West Atlantic species *Strobiligera gaesona* (Dall, 1927) (Fernandes & Pimenta 2019b: fig. 29g), which shows two, three or four cusps in the overcrowded teeth (usually three cusps, one smaller); although not observed by the authors, apparently there is a differentiated, small central tooth with three unequal cusps (Fernandes & Pimenta 2019b: fig. 29b). The teeth of *S. cf. ibex* have three cusps, except the supposed central tooth, with two cusps (Fig. 20F). Remarkably, the outer marginal teeth of *I. obliqua* are very similar to usual teeth from *Strobiligera*, often with three cusps (one of which reduced), evidencing their kinship.

Based on current knowledge, I follow Fernandes & Pimenta (2014) and formalize *Norephora* Gründel, 1975 syn. nov. as a junior synonym of *Subulophora* Laseron, 1958; *Hypotriphora* Cotton & Godfrey, 1931 and *Inella* Bayle, 1879 might be further considered in this genus as well (nomenclatural priority to *Inella*), which would confirm the synonymy of *Norephora* and *Inella* as proposed by Landau *et al.* (2018), but this still requires additional knowledge for the protoconch of the type species of *Inella*. *Strobiligera* Dall, 1924 is probably a recent group, apparently restricted to deep waters of the Atlantic Ocean. Although planktotrophic species of *Subulophora* were also recorded in the Atlantic at the Miocene and before, I am unaware whether this genus is still extant in the Atlantic through some non-planktotrophic species (such as those currently under its possible senior synonym, *Inella*), especially regarding those present in the upper 200 m of depth. Thus, I avoid allocating all non-planktotrophic Atlantic species with a late adapical spiral cord on the teleoconch in *Strobiligera*, but only those from deep waters, following the ongoing phylogeny. Of course, many novelties will be revealed after the addition of more DNA sequences, and this prickly taxonomy may suffer changes.

## Acknowledgements

I am very grateful to Drs Philippe Bouchet, Virginie Héros and Philippe Maestrati (MNHN) for the kind invitation to study this material, and for all the help during my visit to the collection. I also thank the team of LABNANO/CBPF (Centro Brasileiro de Pesquisas Físicas), that allowed access to their SEM equipment, and the sector of Herpetology of MNRJ, which allowed access to their camera. Dr Thierry Backeljau (Royal Belgian Institute of Natural Sciences), MSc Hannco Bakker (Naturalis Biodiversity Center) and two anonymous reviewers provided valuable suggestions to improve this study.

## References

- Abbott R.T. 1974. *American Seashells*. 2<sup>nd</sup> ed. Van Nostrand Reinhold, New York.
- Absalão R.S. 1989. Padrões distributivos e zoogeografia dos moluscos da plataforma continental brasileira. Parte III. Comissão Oceanográfica Espírito Santo I. *Memórias do Instituto Oswaldo Cruz* 84 (4): 1–6. <https://doi.org/10.1590/S0074-02761989000800006>
- Albano P.G., Sabelli B. & Bouchet P. 2011. The challenge of small and rare species in marine biodiversity surveys: microgastropod diversity in a complex tropical coastal environment. *Biodiversity and Conservation* 20: 3223–3237. <https://doi.org/10.1007/s10531-011-0117-x>
- Albano P.G., Bakker P.A.J. & Sabelli B. 2019. Annotated catalogue of the types of Triphoridae (Mollusca, Gastropoda) in the Natural History Museum of the United Kingdom, London. *Zoosystematics and Evolution* 95 (1): 161–308. <https://doi.org/10.3897/zse.95.32803>
- Albano P.G., Di Franco D., Azzarone M., Bakker P.A.J. & Sabelli B. 2023. Review of the types of Indo-Pacific Triphoridae (Mollusca, Gastropoda) in the Muséum national d’Histoire naturelle, Paris. *Zoosystema* 45 (2): 13–106. <https://doi.org/10.5252/zoosystema2023v45a2>



- Amitrov O.V. & Zhegallo E.A. 2007. Triphorids (Gastropoda: Triphoridae) from the Upper Eocene of Ukraine. *Paleontological Journal* 41 (4): 370–381. <https://doi.org/10.1134/S003103010704003X>
- Bakker P.A.J. & Albano P.G. 2022. Nomenclator, geographic and stratigraphic distribution of the family Triphoridae (Mollusca: Gastropoda). *Zootaxa* 5088 (1): 1–216. <https://doi.org/10.11646/zootaxa.5088.1.1>
- Beu A.G. 2004. Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 1: Revised generic positions and recognition of warm-water and cool-water migrants. *Journal of the Royal Society of New Zealand* 34 (2): 111–265. <https://doi.org/10.1080/03014223.2004.9517766>
- Bouchet P. 1985. Les Triphoridae de Méditerranée et du proche Atlantique (Mollusca, Gastropoda). *Lavori de la Società italiana di Malacologia* 21: 5–58.
- Bouchet P. & Warén A. 1993. Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda. *Bolletino Malacologico* 3: 579–840.
- Bouchet P., Lozouet P., Maestrati P. & Héros V. 2002. Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* 75 (4): 421–436. <https://doi.org/10.1046/j.1095-8312.2002.00052.x>
- Dall W.H. 1881. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the United States Coast Survey Steamer “Blake”. *Bulletin of the Museum of Comparative Zoology* 9: 33–144. Available from <https://www.biodiversitylibrary.org/page/30291117> [accessed 4 Nov. 2024].
- Dall W.H. 1889a. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer “Blake”, Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding. XXIX – Report on the Mollusca. Part II. Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology* 18: 1–492. Available from <https://www.biodiversitylibrary.org/page/30097263> [accessed 4 Nov. 2024].
- Dall W.H. 1889b. A preliminary catalogue of shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. *United States National Museum Bulletin* 37: 1–232. <https://doi.org/10.5962/bhl.title.25891>
- Dall W.H. 1924. Notes on Molluscan nomenclature. *Proceedings of the Biological Society of Washington* 37: 87–90. Available from <https://www.biodiversitylibrary.org/page/34552611> [accessed 4 Nov. 2024].
- Dall W.H. 1927. Small shells from dredgings off the southeast coast of the United States by the United States Fisheries Steamer “Albatross” in 1885 and 1886. *Proceedings of the United States National Museum* 70: 1–134. <https://doi.org/10.5479/si.00963801.70-2667.1>
- Fernandes M.R. 2024. Triphoridae (Gastropoda) from Martinique sampled by the MADIBENTHOS expedition, with notes on shallow-water species from Guadeloupe. *Zoosystema* 46 (18): 457–503. <https://doi.org/10.5252/zoosystema2024v46a18>
- Fernandes M.R. & Pimenta A.D. 2014. Two species of the genus *Strobiligera* (Caenogastropoda: Triphoridae) with a multispiral protoconch in Southeastern Brazil. *American Malacological Bulletin* 32 (2): 165–172. <https://doi.org/10.4003/006.032.0207>
- Fernandes M.R. & Pimenta A.D. 2015a. Five new species and two records of Triphorinae (Caenogastropoda, Triphoridae) from Brazil. *Zootaxa* 4012 (3): 493–513. <https://doi.org/10.11646/zootaxa.4012.3.5>
- Fernandes M.R. & Pimenta A.D. 2015b. The multispiral protoconch of *Strobiligera torticula* (Dall, 1881) comb. nov. (Gastropoda, Triphoridae). *Journal of Conchology* 42 (2): 213–216.

- Fernandes M.R. & Pimenta A.D. 2017. Synopsis of the deep-sea groups of Triphoroidea (Gastropoda). *Journal of Natural History* 51 (15–16): 853–865. <https://doi.org/10.1080/00222933.2017.1293181>
- Fernandes M.R. & Pimenta A.D. 2019a. Taxonomic review of *Inella* and *Strobiligera* (Gastropoda: Triphoridae) from Brazil. *Zootaxa* 4613 (1): 1–52. <https://doi.org/10.11646/zootaxa.4613.1.1>
- Fernandes M.R. & Pimenta A.D. 2019b. Basic anatomy of species of Triphoridae (Gastropoda, Triphoroidea) from Brazil. *European Journal of Taxonomy* 517: 1–60. <https://doi.org/10.5852/ejt.2019.517>
- Fernandes M.R. & Pimenta A.D. 2020. Unraveling one of the ‘Big Five’: update of the taxonomy of Triphoridae (Gastropoda, Triphoroidea) from Brazil. *European Journal of Taxonomy* 665: 1–170. <https://doi.org/10.5852/ejt.2020.665>
- Fernandes M.R., Salgueiro F., de Paula T.S., Lôbo-Hajdu G. & Pimenta A.D. 2021. Cryptic speciation in the “*Marshallora nigrocincta*” species complex (Gastropoda, Triphoridae) from the Western Atlantic. *Journal of Zoological Systematics and Evolutionary Research* 59 (4): 819–838. <https://doi.org/10.1111/jzs.12461>
- Garcia E.F. & Lee H.G. 2002. Report on molluscan species found in the offshore waters of Louisiana, including many extensions of known range and unnamed species. *American Conchologist* 30: 10–13.
- Garcia E.F. & Lee H.G. 2020. *Report on Molluscan Species Found in the Offshore Waters of Louisiana, Including many Extensions of Known Range and Unnamed Species*. Available from <http://www.jaxshells.org/efg1030.htm> [accessed 4 Nov. 2024].
- Garrigues B. & Lamy D. 2017. Description d’une nouvelle espèce de *Dermomurex* (Muricidae, Muricinae) collectée au cours de l’expédition KARUBENTHOS 2 en Guadeloupe, Antilles Françaises. *Xenophora Taxonomy* 16: 39–43.
- Gofas S., Freiwald A. & Hoffman L. 2023. New species and new records in Cerithiopsidae and Newtoniellidae (Triphoroidea, Gastropoda) from the South Azorean Seamount Chain. *Iberus* 41 (1): 111–148.
- Harasewych M.G., Uribe J.E. & Fedosov A.E. 2020. *Costapex baldwinae*, a new species of bathyal costellariid (Mollusca: Gastropoda: Neogastropoda: Costellariidae) from the Caribbean Sea. *Proceedings of the Biological Society of Washington* 133: 134–141. <https://doi.org/10.2988/20-00010>
- Lamy D. & Pointier J.P. 2018. *Marine and Freshwater Molluscs of the French Caribbean. Volume I*. PLB Editions, Guadeloupe.
- Landau B.M., La Perna R. & Marquet R. 2006. The early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 6: Triphoroidea, Epitonioidae, Eulimoidea. *Palaeontos* 10: 1–96.
- Landau B.M., Ceulemans L. & Van Dingenen F. 2018. The upper Miocene gastropods of northwestern France, 2. Caenogastropoda. *Cainozoic Research* 18 (2): 177–368.
- Laseron C.F. 1958. The family Triphoridae (Mollusca) from northern Australia; also Triphoridae from Christmas Island (Indian Ocean). *Australian Journal of Marine and Freshwater Research* 9 (4): 569–658. <https://doi.org/10.1071/MF9580569>
- Lauridsen B.W. & Schnetler K.I. 2014. A catalogue of Danian gastropods from the Baunekule facies, Faxe Formation, Denmark. *GEUS Bulletin* 32: 1–117. <https://doi.org/10.34194/geusb.v32.4593>
- Leal J.H. 2021. Type specimens in the molluscan collection of the Bailey-Matthews National Shell Museum, Florida, USA. *Zootaxa* 4951 (1): 1–40. <https://doi.org/10.11646/zootaxa.4951.1.1>
- Lozouet P. 1999. Nouvelles espèces de gastéropodes (Mollusca: Gastropoda) de l’Oligocène et du Miocène inférieur d’Aquitaine (sud-ouest de la France). Partie 2. *Cossmanniana* 6: 1–68.

- Lozouet P., Lesport J.-F. & Renard P. 2001. Revision des Gastropoda (Mollusca) du Stratotype de l'Aquitainien (Miocene inf.): Site de Saucats "Lariev", Gironde, France. *Cossmanniana, New Series* 3: 1–189.
- Marquet R. 1996. The family Triphoridae in the Neogene of Belgium (Mollusca, Gastropoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 66: 137–149.
- Marshall B.A. 1983. A revision of the recent Triphoridae of Southern Australia (Mollusca: Gastropoda). *Records of the Australian Museum*, Suppl. 2: 1–119. <https://doi.org/10.3853/j.0812-7387.2.1983.102>
- Marshall B.A. 1994. An unusual triphorid (Mollusca: Gastropoda) from the Moluccas, Indonesia. *Zoologische Mededelingen* 68 (4): 39–43.
- MolluscaBase 2023. Available from <https://www.molluscabase.org> [accessed 4 Nov. 2024].
- Mulochau T., Huet R., Trentin F., Rauby T., Holon F., Ballesta L. & Durville P. 2020. Inventaire des mollusques du Mont sous-marin La Pérouse – Ile de La Réunion, sud-ouest Océan Indien – Expédition La Pérouse 2019. *Folia Conchyliologica* 55: 1–13.
- Nava M.L. & Severejn H.J. 2010. Variación espacial del macrobentos intermareal en playas arenosas de alta energía del noroeste del Golfo de Venezuela. *Ciencia* 18 (4): 235–246.
- Poupin J. & Corbari L. 2016. A preliminary assessment of the deep-sea Decapoda collected during the KARUBENTHOS 2015 Expedition to Guadeloupe Island. *Zootaxa* 4190 (1): 1–107. <https://doi.org/10.11646/zootaxa.4190.1.1>
- Rabiller M. & Richard G. 2019. Conidae offshore de Guadeloupe: description du matériel dragué lors de l'expédition KARUBENTHOS 2 contenant de nouvelles espèces. *Xenophora Taxonomy* 24: 3–31.
- Redfern C. 2013. *Bahamian Seashells: 1161 Species from Abaco, Bahamas*. Bahamian Seashells Inc., Boca Raton, FL, USA.
- Rios E. 1985. *Seashells of Brazil*. Museu Oceanográfico da FURG, Rio Grande.
- Rios E. 1994. *Seashells of Brazil. 2<sup>nd</sup> ed.* Museu Oceanográfico da FURG, Rio Grande.
- Rios E. 2009. *Compendium of Brazilian Seashells*. Evangraf, Rio Grande.
- Rolán E. & Fernández-Garcés R. 2007. Caribbean Triphoridae (Gastropoda: Triphoroidea): list and colour illustrations. *Neptunea* 6 (3): 13–24.
- Rolán E. & Fernández-Garcés R. 2008. New data on the Caribbean Triphoridae (Caenogastropoda, Triphoroidea) with the description of 26 new species. *Iberus* 26 (1): 81–170.
- Rolán E. & Fernández-Garcés R. 2015. Triphorids of the Karubenthos Expedition to Guadeloupe Island. *Gloria Maris* 54 (2): 46–54.
- Rosenberg G., Moretzsohn F. & Garcia E. 2009. Gastropoda (Mollusca) of the Gulf of Mexico. In: Felder D. & Earle S. (eds) *Gulf of Mexico Origin, Waters and Biota*: 579–699. Texas A&M University Press, College Station, TX, USA.
- Schnetler K.I., Madsen H., Śliwińska K.K., Heilmann-Clausen C. & Ulleberg K. 2024. A late Oligocene molluscan fauna and Oligocene coastal outcrops from Vilsund, NW Denmark. *Bulletin of the Geological Society of Denmark* 73: 1–40. <https://doi.org/10.37570/bgds-2024-73-01>
- Severejn H.J., Nava M. & Severejn Y.G. 2017. Marine biodiversity gastropods surveys as a model for early detection of exotic-invaders species. *Oceanography & Fisheries* 3 (5): e555625. <https://doi.org/10.19080/OFOAJ.2017.03.555625>
- Simone L.R.L. 2006. A new Triphoridae from Canopus Bank, N.E. Brazil (Caenogastropoda). *Strombus* 13 (1): 6–8.

*Manuscript received: 19 February 2024*

*Manuscript accepted: 26 August 2024*

*Published on: 11 December 2024*

*Topic editor: Magalie Castelin*

*Section editor: Thierry Backeljau*

*Desk editor: Pepe Fernández*

Printed versions of all papers are deposited in the libraries of four of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.